THE RESPONSE OF

PLANT COMMUNITY STRUCTURE AND PRODUCTIVITY

TO CHANGES IN HYDROLOGY IN ALASKAN BOREAL PEATLANDS

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Abstract

Northern peatlands have been a long-term sink for atmospheric CO_2, and have had a net cooling effect on global climate for the last 8,000 to 11,000 years. Across Alaska, peatlands face increased effects of climate change through hydrologic disturbance, both drying and flooding, and these conditions alter the ability of peatlands to accumulate carbon. Here, I examined the influence of changing hydrology in a moderate rich fen and a bog located in the discontinuous permafrost zone of interior Alaska. In both sites, I quantified how changing hydrology affected vegetation composition and ecosystem carbon uptake. At the fen, drying via a lowered water table treatment caused larger changes in vegetation composition and primary productivity than flooding via a raised water table treatment. In the bog, an area of recent permafrost thaw (collapse scar) had increased rates of understory net primary production and gross primary production, relative to an adjacent but older collapse scar and the surrounding permafrost plateau. Together, results from these studies highlight possible community responses to projected change in water availability, whether through drying or flooding, and demonstrate initial mechanisms for community responses altering ecosystem processes.

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Chapter 1
I. Introduction

Overview of study objectives

Water availability in Alaskan peatlands is changing at both regional and local scales. How individual peatlands will respond to these changes in water availability depends on factors such as average precipitation, peat density, local vegetation composition, and microtopography (Bubier et al., 1999). Few studies have examined the impact of both wetting and drying on peatland vegetation and little is known about the sensitivity of Alaskan peatlands to changing hydrology. Many studies investigating the consequences of peatland drying have focused on the effects of anthropogenic drainage, such as drainage associated with peat harvesting in post-glacial peatlands in the Canadian interior (Strack et al., 2006), or silviculture in Finnish peatlands (Murphy et al., 2009). There are few studies that have examined the effects of flooding in peatlands, though several studies have targeted the effects of flooding caused by permafrost thaw and subsequent thermokarst on peatland vegetation and carbon cycle processes (Camill et al., 2001; Myers-Smith et al., 2007; Turetsky et al., 2007; Wickland et al., 2006). The overall goal of this study was to characterize the response of peatland vegetation to both drying and flooding in interior Alaska, and to explore how changes in plant functional group abundance affects rates of primary productivity.

Climate change in Alaska

Over the last 50 years, Alaska has experienced rapid and directional climate change (Chapin et al., 2010; Hinzman et al., 2005; Osterkamp and Romanovsky, 1999). For the boreal region of Alaska, mean annual air temperature has increased 1.3 °C over the past 50 years, associated with earlier spring thaw and a prolonged growing season (Euskirchen et al., 2009; Hinzman et al., 2005). These changes have had ecological impacts such as earlier bud setting and leaf out for primary producers (Linderholm, 2006), as well as earlier nesting, shifts in migration, and altered range areas observed in a number of bird species (Hinzman et al., 2005).

Changes in climate have had a strong influence on high latitude soils. Currently, the Alaskan boreal forest region is underlain by discontinuous permafrost, where permafrost is common on north-facing slopes, valley bottoms and in peatlands. Surface permafrost distributions are currently influenced by thaw at rates as high as 0.1 m yr^{-1} near the southern limit of discontinuous permafrost in Alaska (Osterkamp et al., 2000; Osterkamp and Romanovsky, 1999). Air temperature warming also has triggered warming in deeper permafrost layers in many locations across Alaska (Osterkamp and Romanovsky, 1999).

Air temperature across the boreal forest is projected to increase an additional 3-7 °C by the end of the 21st century (Chapin et al., 2010; Jorgenson et al., 2001). Because of this, surface permafrost throughout much of the sporadic and discontinuous permafrost zones is predicted to thaw completely within the next 100 years, although deeper permafrost may exist for millennia (Camill, 2005; Osterkamp and Romanovsky, 1999).

Introduction to peatlands

Peatlands are ecosystems that have at least 40 cm of peat (Rydin and Jeglum, 2006). Peat is mostly dead plant material in various stages of decomposition. By definition, peat is at least 20-30% organic material by mass, but frequently is more than 80% organic matter content. Due to high organic matter content, peat also tends to be acidic with low bulk density (< 0.3 g / cm^3) (Reddy and DeLaune, 2008).

There are two main types of peatlands: fens and bogs. Fens are minerotrophic, receiving ground and / or surface water that interacts with mineral soils. Fens may be further divided along gradients of species diversity and nutrient availability from poor fens to extreme rich fens. Bogs are ombrotrophic, receiving water inputs from precipitation, and consequently are typically nutrient poor with low pH. Differences in plant composition between bogs and fens have been well documented throughout the North American boreal zone (Camill, 1999; Jorgenson et al., 2001; Locky et al., 2005; Moore et al., 2002).Vegetation dominating boreal fens often include sedges (*Carex* sp.), spiked rushes (*Eleocharis* sp.), *Sphagnum riparium*, and brown mosses such as

Drepanocladus aduncus and *Hamatocaulis vernicosus* (Vitt, 2006). Vegetation in boreal bogs usually includes black spruce (*Picea mariana*), *Ledum* spp., and *Sphagnum* or feather mosses (Vitt and Chee, 1990).

Globally, peatlands exist in areas where precipitation exceeds evapotranspiration and groundwater losses, and can be found in most biomes. Peatlands cover approximately 3-5% of the total Earth surface (Gorham, 1991). However, more than 80% of peatlands are located in northern regions (Yu et al., 2010), covering 24% of land in the circum-boreal forest, (Vitt, 2006). In Alaska, peatlands cover at least 8% of total land area (132,000 km^2; Bridgham et al., 2006); although this estimate likely underestimates peatland abundance associated with lowland black spruce forests.

Peatlands sequestered CO_2 throughout the Holocene with the accumulation of organic soils and carbon storage as peat, currently storing one third of the terrestrial carbon pool (Gorham, 1991; Blodau, 2002). Today pristine peatlands are thought to serve as a small net CO_2 sink, but also serve as a source of atmospheric CH_4 and CO (Blodau, 2002). Using a mean peat accumulation rate of 19.4 g C / m^2 (Vitt et al., 2000), Alaska peatlands are estimated to take up 2.6 Tg C / yr from the atmosphere.

Effects of climate change on peatland hydrology

Warming air temperatures across boreal Alaska will create an increase in evapotranspiration rates. Increased evapotranspiration without a subsequent increase in precipitation can create soil water deficits to lower the water table position in peatlands. A second mechanism of drying results from abrupt drainage of soils associated with permafrost thaw, as areas of talik are created and connect to groundwater transport systems allowing sub-surface water flow during winter months (Muskett and Romanovsky, 2011). Evidence for draining via these drying mechanisms has been observed in lakes and ponds in the Yukon Flats and near Council, Alaska (Riordan et al., 2006; Yoshikawa and Hinzman, 2003). Ecologically, drying lowers the position of the water table relative to the peat surface within peatlands, thereby exposing more organic soils to aerobic respiration as the water table drops deeper into the soil column.

While the majority of soils in the boreal region are likely to experience increased soil moisture deficits with future climate change, wetlands in interior Alaska will potentially experience increased flooding due to predicted changes in snowpack depths, thermokarst, and increased runoff via meltwater from higher elevations. Flooding often occurs in floodplains during spring thaw, though future changes in snowpack depth and timing of spring thaw could alter these flooding patterns (Muskett and Romanovsky, 2011; Euskirchen et al., 2009). In interior Alaska, peatlands are often underlain by permafrost, and thermokarst formation with soil inundation can occur where ice rich permafrost begins to thaw. Ecological consequences of thaw include a ground subsidence averaging 1-2 m, thereby increasing water availability within collapsed areas relative to the surrounding permafrost plateau (Camill, 2005; Hinzman et al., 2005; Jorgenson et al., 2001; Osterkamp and Romanovsky, 1999; Osterkamp et al., 2000). Change in water availability then alters the associated plant community composition and may permanently alter trajectories of succession across the landscape, as thermokarst formation facilitates a change from terrestrial ecosystem types to aquatic and wetland systems (Osterkamp et al., 2000; Racine et al., 1998). In the Tanana Flats region of interior Alaska, 42% of the land area that supports or supported surface permafrost in the recent past has been affected by thermokarst formation. Additionally, the rate of permafrost thaw in peatlands in this region has increased by 8% in the past 46 years (Jorgenson et al., 2001).

Effects of disturbance on plant production in peatlands

Previous studies exploring the influences of disturbance on peatlands have focused on inter-annual variation in climate or have used manipulations to simulate drought or flooding (Laine et al., 1995; Weltzin et al., 2000). Short term changes in water availability related to immediate change in environmental conditions are likely to influence ecosystem and community responses differently than prolonged or permanent changes. Short term changes in hydrology can influence carbon uptake via photosynthesis, and may impact energy allocation into above- or below- ground tissue (**Figure 1.1**). In general, wetter conditions in the short term have increased gross primary

productivity (GPP), net primary productivity (NPP) and biomass, while drier conditions have reduced GPP, NPP and biomass (Chivers et al., 2009; Moore et al., 2002; Updegraff et al., 2001; Weltzin et al., 2000). However, responses are dependent on microform, or small localized differences in topography such as a hummock or hollow. Microforms elevated above the water table (hummocks) generally have increased GPP and NPP during drier conditions, while lawns or hollows have reduced carbon uptake during dry periods (Alm et al., 1997; Strack et al., 2006). This is primarily related to differences in species between microforms, as shrubs and other drought tolerant species are present on hummocks while aquatic hydrophilic species typically dominate hollows and lawns. Over longer time periods, community compositional changes with prolonged drainage or drying may also influence productivity. Studies have shown an increase in tree and shrub biomass and NPP at the expense of moss NPP and biomass (Laine et al., 1995; Murphy et al., 2009). Despite measurements of change in NPP, few studies have examined changes in species composition and succession in conjunction with drying or flooding in peatlands.

Multiple studies have found significant differences in species composition between permafrost plateaus and adjacent collapse scars (Beilman, 2001; Camill et al., 2001). Generally, permafrost plateaus are dominated by shrubs and/or tree species, while the collapse scars are dominated by more aquatic species with hydrophilic mosses such as *Sphagnum riparium*. Biomass typically is greater in permafrost plateaus than in collapse scars associated with trees; however there may be no differences in NPP before and after permafrost thaw due to tradeoffs between woody tissue growth and moss growth (Camill et al., 2001).

Research questions

The focus of my research was to examine the influence of changing hydrological conditions on vegetation composition and productivity in an Alaskan peatlands. Chapter 2 focuses on the effects of drying, wetting and thermokarst on plant species composition, primary productivity and plant biomass in a bog and a rich fen. Chapter 3 links changes

in gross primary productivity (GPP) at these study sites to light and water availability, and plant community structure. In Chapter 4, I review how plant community composition has influenced NPP and GPP, and make conclusions about what my results mean for the vulnerability of peatlands to future climate change.

Specific questions and predictions addressed in Chapter 2:

(1) In a rich fen, does flooding or drying of the peat prompt a greater change in plant species composition and productivity?

I predict that flooding of fen vegetation will cause a more rapid change in plant community structure than drying, with increased presence of wetland obligate species under the flooded conditions. However I predict that productivity will change more with drying than with flooding as limitations in water availability for the moss layer will reduce ecosystem NPP substantially with no immediate offset in increased shrub abundance or productivity.

(2) How does time since thermokarst thaw influence plant community structure and productivity?

I predict that there will be differences in plant species composition between the permafrost plateau and collapse scars. The permafrost plateau will have a high abundance of understory shrubs and tree seedlings, while the collapse scars will have aquatic sedges and forbs. However, tradeoffs in new growth between mosses and woody species will result in no differences in productivity between the permafrost plateau and collapse scars.

Specific questions and predictions addressed in Chapter 3:

(1) How does GPP vary between a rich fen and a bog, and how is GPP within each site influenced by hydrologic disturbance?

I predict that under pristine conditions, the fen will have higher GPP than the bog, due to greater nutrient availability. Between water table manipulation plots at the fen, I expect reduced GPP in the lowered treatment due to water stress. I also expect GPP

to increase in the raised water table treatment due to a lack of water stress on the plant community. For the bog I predict that understory GPP will be lower in the peat plateau (permafrost plot) than the thermokarst areas, due to drier and colder soil conditions that limit nutrient availability for plant growth.

(2) How do environmental controls on GPP vary between these sites and types of disturbance?

I expect that the fen will show higher levels of light-saturated photosynthesis than the bog associated with a higher availability of nutrients in the fen. Within the fen I expect that the raised plot will have the highest light saturated photosynthesis related to the reduced potential for water stress, while the lowered plot should have the lowest light saturated photosynthesis. At the bog the understory of the permafrost plateau should show the lowest light saturated photosynthesis, associated with a shade tolerant community structure. I predict that optimal water table position for maximum GPP will be deepest for the lowered plot at the fen and shallowest for the raised plot. At the bog I predict the optimal water table position will be deeper for the peatland plateau than for the thermokarst areas.

(3) How do plant community controls on GPP differ among these sites and types of hydrological disturbance?

Between the bog and the fen I predict that vascular contributions to GPP will depend on plant growth form. Sedges and grasses will contribute more to GPP in the fen, while shrubs will contribute more to GPP at the bog. I predict that mosses will contribute more to understory GPP than vascular species at the bog, especially for the thermokarst formations, while shrubs will be the most important contributors to GPP at the permafrost plateau. For the fen I predict that differences in understory GPP will depend on differences in vascular plant abundance. Sedge and grass contributions to understory GPP will be high in the control and raised plots, while shrub contributions to GPP will be high in the lowered plot.

II. Literature cited

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykanen, H., & Martikainen, P. J. (1997). Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia, 110(3),* 423-431.

Beilman, D. W. (2001). Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada. *Canadian Journal of Botany, 79(8),* 983-993.

Blodau, C. (2002). Carbon cycling in peatlands — A review of processes and controls. *Environmental Review, 10(2),* 111-134.

Bridgham, S. D., P. Megonigal, J., Keller, J. K., Bliss, N. B., & Trettin, C. (2006). The carbon balance of North American wetlands. *Wetlands, 26(4),* 889-913.

Bubier, J. L., Frolking, S., Crill, P. M., & Linder, E. (1999). Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *Journal of Geophysical Research, 104(D22),* 27683-27692.

Camill, P. (1999). Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany, 77(5),* 721-733.

Camill, P. (2005). Permafrost thaw accelerates in boreal peatlands during late-20th century climate warming. *Climatic Change, 68(1-2),* 135-152.

Camill, P., Lynch, J. A, Clark, J. S., Adams, J. B., & Jordan, B. (2001). Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems, 4(5),* 461-478.

Chapin, F. S., McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., Kasischke, E.S., Euskirchen, E.S., Jones, J.B., Jorgenson, M. T., Kielland, K., Kofinas, G. P., Turetsky, M. R., Yarie, J., Lloyd, A. H., & Taylor, D. L. (2010). Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research, 40(7),* 1360-1370.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2009). Effects of experimental water table and temperature manipulations on ecosystem CO_2 fluxes in an Alaskan rich fen. *Ecosystems*, *12(8),* 1329-1342.

Euskirchen, E. S., McGuire, A. D., Chapin, F. S., Yi, S., & Thompson, C. C. (2009). Changes in vegetation in northern Alaska under scenarios of climate change, 2003-2100: implications for climate feedbacks. *Ecological Applications*, *19(4),* 1022-43.

Gorham, E. (1991). Northern peatlands: role in the carbon cycle and probable responses to climatic warming. *Ecological Applications*, *1(2),* 182-195.

Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin, F. S., Dyurgerov, M. B., Fastie, C. L., Griffin, B., Hollister, R. D., Hope, A., Huntington, H. P., Jensen, A. M., Jia, G. J., Jorgenson, T., Kane, D. L., Klein, D. R., Kofinas, G., Lynch, A. H., Lloyd, A. H., McGuire, A. D., Nelson, F. E., Oechel, W. C., Osterkamp, T. E., Racine, C. H., Romonovsky, V. E., Stone, R. S., Stow, D. A., Sturm, M., Tweedie, C. E., Vourlitis, G. L., Walker, M. D., Walker, D. A., Webber, P. J., Welker, J. M., Winker, K. S., & Yoshikawa, K. (2005). Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, *72(3),* 251-298.

Jorgenson, T. M., Racine, C. H., Walters, J. C., & Osterkamp, T. E. (2001). Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, *48(4)*, 551-579.

Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in Southern Finland. *The Journal of Applied Ecology*, *32(4),* 785.

Linderholm, H. (2006). Growing season changes in the last century. *Agricultural and Forest Meteorology*, *137(1-2),* 1-14.

Locky, D. A., Bayley, S. E., & Vitt, D. H. (2005). The vegetational ecology of black spruce swamps, fens, and bogs in southern boreal Manitoba, Canada. *Wetlands*, *25(3),* 564-582.

Moore, T. R., Bubier, J. L., Frolking, S. E., Lafleur, P. M., & Roulet, N. T. (2002). Plant biomass and production and CO_2 exchange in an ombrotrophic bog. *Journal of Ecology*, *90(1),* 25-36.

Murphy, M., Laiho, R., & Moore, T. R. (2009). Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems, 12(8),* 1268-1282.

Muskett, R. R., & Romanovsky, V. E. (2011). Alaskan permafrost groundwater storage changes derived from GRACE and ground measurements. *Remote Sensing, 3(2),* 378-397.

Myers-Smith, I. H., McGuire, A. D., Harden, J. W., & Chapin, F. S. (2007). Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest. *Journal of Geophysical Research, 112(G4),* 1-11.

Osterkamp, T. E., & Romanovsky, V. E. (1999). Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes, 10(1),* 17-37.

Osterkamp, T. E., Viereck, L., Shur, Y., Jorgenson, M. T., Racine, C. H., Doyle, A., & Boone, R. D. (2000). Observations of thermokarst and its impact on boreal forests in Alaska. *Arctic, Antarctic, and Alpine Research, 32(3),* 303-315.

Racine, C. H., Jorgenson, M. T., & Walters, J. C. (1998). Thermokarst vegetation in lowland birch forests on the Tanana Flats, interior Alaska, U.S.A. *Permafrost-Seventh International Conference* (pp. 927-933).

Reddy, R., & DeLaune, R. D. (2008). Biogeochemistry of wetlands: science and applications. p. 22. Taylor & Francis Group, Boca Raton, FL, USA.

Riordan, B., Verbyla, D., & McGuire, A. D. (2006). Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research, 111(G4).*

Rydin, H.,& Jeglum, J. (2006). The biology of peatlands. Oxford University Press, Oxford.

Strack, M., Waddington, J. M., Rochefort, L., & Tuittila, E. S. (2006). Response of vegetation and net ecosystem carbon dioxide exchange at different peatland microforms following water table drawdown. *Journal of Geophysical Research, 111(G2),* 1-10.

Turetsky, M. R., Wieder, R. K., Vitt, D. H., Evans, R. J., & Scott, K. D. (2007). The disappearance of relict permafrost in boreal North America: effects on peatland carbon storage and fluxes. *Global Change Biology, 13(9),* 1922-1934.

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., & Harth, C. (2001). Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecological Applications, 11(2),* 311-326.

Vitt, D. H. (2006). Functional characteristics and indicators of boreal peatlands. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal Peatland Ecosystems* (Vol. 188, pp. 9-24). Springer-Verlag Berlin Heidelberg.

Vitt, D. H., & Chee, W. L. (1990). The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio, 89(2),* 87-106.

Vitt, D. H., Halsey, L. A, Bauer, I. E., & Campbell, C. (2000). Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences, 37(5),* 683-693.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., & Chapin, C. T. (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology, 81(12),* 3464-3478.

Wickland, K. P., Striegl, R. G., Neff, J. C., & Sachs, T. (2006). Effects of permafrost melting on CO_2 and CH_4 exchange of a poorly drained black spruce lowland. *Journal of Geophysical Research, 111(G2),* 1-13.

Yoshikawa, K., & Hinzman, L. D. (2003). Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near council, Alaska. *Permafrost and Periglacial Processes, 14*(2), 151-160.

Yu, Z., Loisel, J., Brosseau, D. P., Beilman, D. W., & Hunt, S. J. 2010. Global peatland dynamics since the Last Glacial Maximum. *Geophysical Research Letters, 37(L13402).*

III. Figures and Tables

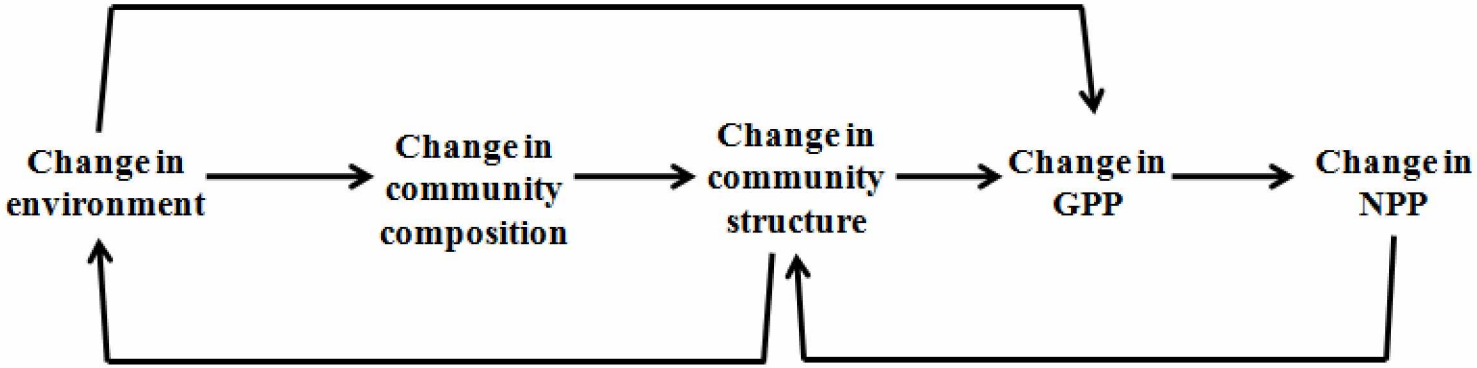

Figure 1.1 Conceptual framework illustrating connections between environmental conditions, subject to influence associated with changes in climate and disturbance, and ecosystem productivity processes. Chapter 2 addresses the influence of change in environment on community composition, structure and net primary productivity (NPP), while Chapter 3 addresses how both the environment and community structure may influence gross primary productivity (GPP).

Chapter 2
Shifts in plant community structure and productivity in two Alaskan boreal peatlands in response to hydrologic disturbance

I. Abstract

Current and future increases in air temperatures will influence boreal ecosystems directly and indirectly via altering hydrology. I examined vegetation responses to changing hydrology in a bog and fen located in the Tanana River floodplain of interior Alaska. At the fen, I examined the effects of 5 years of water table manipulation (including both drying and flooding) on plant species composition, biomass and productivity. At the bog I examined the effects of time since permafrost thaw on plant species composition, biomass and productivity. At both sites, I quantified species abundance, aboveground biomass, above- and below-ground net primary productivity (NPP), and vascular green area (VGA). In the fen, species composition in the lowered (drought) and raised (flooding) water table manipulations differed from the control treatment. Sedges increased in cover in the raised plot, while forbs and deciduous shrubs increased in the lowered plot relative to the control. However, total biomass and NPP did not vary between the experimental and control treatments, though VGA was greater in the lowered treatment than in either the control or raised treatments. In the bog there were large differences in species composition, biomass and productivity between the permafrost plateau and collapse scar bogs. More recent permafrost thaw was associated with greater aboveground biomass and a higher total NPP than an area of older thaw. Overall, my results at the fen showed that shifts in community composition were more sensitive to 5 years of manipulation changes in hydrology than was biomass or productivity. My results at the bog showed that permafrost thaw results in large changes in plant species composition and productivity, and provides some insights into the nature of successional changes following permafrost thaw.

II. Introduction

Northern latitudes are experiencing increases in air temperature that are predicted to continue over the next century. Air temperatures across Alaska have increased 1.3 °C in the past 50 years (Chapin et al., 2010) with rapid changes evident since the late 1970s (Hansen et al., 2006; Osterkamp et al., 2009). Future predictions suggest increases in annual temperatures between 3-7 °C in the next century (Walsh et al., 2008). In addition to the direct impacts of warming on ecosystem processes, there are likely indirect impacts on terrestrial systems via changes in water availability. Increases in evapotranspiration, permafrost thaw and sub-surface water flow are all predicted to occur with warming, and are likely to influence northern ecosystems (Hinzman et al., 2005; Osterkamp et al., 2000; Riordan et al., 2006).

Northern peatlands, many of which are underlain with permafrost, are particularly vulnerable to climate change. Not only are they situated in regions experiencing rapid climate change, they also are comprised of species that grow in moist ecosystems, including a dominance of hydrophilic mosses (Vitt, 2006). Peat accumulation and continued carbon storage in peatlands is dependent on anaerobic conditions, largely controlled by the water table position, which limits decomposition (Blodau, 2002). Thus declines in water table position as a result of climate change could stimulate peat decomposition and further limit peat accumulation. However, there are several stabilizing mechanisms in peatlands that may cause these ecosystems to be resilient to climate change. One such mechanism is the subsidence of non-rigid surface peat in response to lower water position, which effectively maintains the peat surface at a similar depth relative to the water table (Strack and Waddington, 2007). Another involves the high water retention traits of *Sphagnum* species, which can maintain moist surface soils even during drought (Andrus, 1986).

On landscape or regional scales, losses in peatland area related to drying may be offset by terrestrialization of former ponds and lakes (Roach et al., 2011) or collapse scar formation and expansion associated with permafrost disturbance and thermokarst (Jorgensen et al., 2010). For example, within the Tanana Flats of interior Alaska, peatland

expansion as a result of surface permafrost thaw is substantial: fen area increased 29% between 1949 and 1995, while collapse scars and bogs increased in area by 8% (Jorgenson et al., 2001).

A variety of techniques have been used to examine the effects of climate change, in particular changes in water availability, on peatland vegetation and carbon cycling. Many studies have examined the effects of changing temperature and moisture content in peatlands using microcosms to examine responses in soil decomposition, but have largely ignored issues related to vegetation. A common garden experiment that controlled the climate above peat mesocosms found that an increase in water table position (wetting) stimulated aboveground NPP, while a decrease in water table position (drying) increased belowground NPP (Updegraff et al., 2001; Weltzin et al., 2000). Individual plant growth forms responded differently to change in water availability, with increases in moss, graminoids and forb productivity and decreases in shrub productivity under wet conditions (Welzin et al., 2000).

Finally, several studies have characterized peatland succession following drainage for forestry. These studies tend to show a decrease in vegetation diversity at the landscape level (gamma diversity) despite little overall change in diversity within individual peatlands (alpha diversity) as aquatic and lawn species are replaced by shrubs and trees (Laine et al., 1995). In general, sustained drying has increased aboveground tree and shrub biomass and decreased moss cover and productivity (Murphy et al., 2009; Laine et al., 1995). The increases in productivity in drained areas have also contributed to increases in peat accumulation (Laine et al., 1996). Collectively, these techniques have highlighted that changes in peatland carbon cycling, and peat accumulation rates in response to changing hydrology, are likely to be mediated by vegetation.

While boreal peatlands are expected to experience more drought and lower water table positions under future climate change scenarios, changes in peatland hydrology with climate may also be associated with flooding. These flooding conditions are linked with thaw of surface permafrost and subsequent thermokarst with collapse scar formation, as ground subsidence allows inundation of the full soil profile (Osterkamp et al., 2000). The

effect of this naturally induced flooding on the peatlands has been demonstrated by examining differences in plant community composition between peatlands underlain by permafrost (which can occur as permafrost plateaus, palsas, or pingos) and those that have experienced permafrost thaw (i.e. collapse scars or internal lawns) (Beilman, 2001). For example, permafrost thaw in peat plateaus changes community structure from one dominated by black spruce (*Picea mariana)* and feather moss to collapse scars dominated by *Sphagnum* and sedges (*Carex spp.*). These studies also have shown that areas with intact permafrost have greater aboveground biomass but lower NPP relative to the thaw features (Camill et al., 2001; Camill and Clark, 1998).

The majority of experiments examining peatland responses to climate change have been conducted in *Sphagnum*-dominated bogs and fens. Few studies have quantified the sensitivity of rich fen vegetation or carbon cycling processes to environmental change. However, rich fens are one of the most dominant peatland types across the North American boreal biome (Vitt, 2006). One objective of this study was to characterize the response of vegetation community structure and productivity to a water table manipulation in a rich fen in interior Alaska. The manipulation included both drying (lowered water table) and flooding (raised water table) treatments. Two years after the onset of the manipulation, there were no observed changes in the vegetation community structure, although reductions in gross primary productivity were evident in the lowered treatment plot relative to the control plot (Chivers et al., 2009). A component of my study examined whether changes in vegetation occurred following 5 years of water table manipulation in this rich fen. The second objective of this study was to characterize the effects of permafrost thaw on plant community composition, biomass and productivity within a bog. My study is the first to examine the influence of time since thaw on ecosystem and community functions because of the establishment of plots in two collapse scars of different ages.

By focusing this study on both the bog and fen site, I was able to ask two main questions: (1) At the fen water table manipulations, does flooding or drying prompt a

greater change in plant community structure and productivity? (2) How does time since permafrost thaw influence plant community structure and productivity?

III. Methods

Study site

My research was conducted at the Alaskan Peatland Experiment (APEX) located adjacent to the Bonanza Creek Experimental Forest (BCEF), approximately 35 km southwest of Fairbanks, AK (64.82° N, 147.87° W). All sites contained in this study are situated approximately 1 km apart from one another, and lack any major changes in topography. A 50 year average for precipitation in the Fairbanks region is 287 mm, while mean annual temperature (1917-2000) averages -3.1°C (Hinzman et al., 2006).

The APEX study area includes a moderate rich fen, where three water table position manipulations were established in 2005, including a control, a lowered and a raised water table plot (Chivers et al., 2009). Water table manipulation plots have been maintained annually via pumping groundwater, from approximately snow melt until freeze up. On average the lowered plot has remained ~10 cm below the control plot while the raised plot has been ~5 cm above the control plot (Chivers et al., 2009; Kane et al., 2010; Turetsky et al., 2008). Despite differences in mean growing season water table position, all three plots experienced short term fluctuations in response to rain events, as well as a seasonal drawdown that is typical of the site. All plots at the fen have no surface permafrost (in the top 2 m), with seasonal ice that thaws between mid July and late August. Vegetation across manipulation plots was similar prior to water table manipulation initiated in 2005. Previous papers have reported results regarding the effects of these water table manipulations on CO_2, CH_4 and DOC after two years of experimentation (Chivers et al., 2009; Kane et al., 2010; Turetsky et al., 2008).

The APEX study area also includes a peat plateau bog site that has several internal collapse scars that formed with thaw of surface permafrost. The peat plateau forest matrix was designated as the stable permafrost plot (referred to hereafter as the permafrost plot) within which two collapse scar features were present. I used observed

changes in land features between photographs to determine that one collapse scar thawed between 1972 and 1983 (hereafter referred to as the old collapse plot), while the second formation appeared between 1983 and 1994 (hereafter referred to as the new collapse plot). Plot area within the collapse scars was calculated from survey coordinate points measured in 2007, using the 3-D modeling program Rhinoceros 4 (Rhinoceros 4: NURBS modeling for Windows © 1993-2008 Robert McNeel & Associates). I determined the area for the old collapse plot as 1528 m^2 for the new collapse plot and 819 m^2.

Field methods

CLIMATE AND ENVIRONMENTAL VARIABLES

At each site, climate data (air temperature, relative humidity and precipitation) were collected continuously using CR10X dataloggers (Campbell Scientific Inc., Logan, UT). I collected soil temperature data at each plot within both the bog and fen sites (0 cm, 2 cm, 10 cm, and 25 cm below ground surface) using thermisters. There were three soil temperature stations within each water table treatment at the fen, while the bog plots contained one or two stations each (n = 1 at the permafrost plot, n = 2 at the new collapse plot, n = 2 at the old collapse plot). Water table measurements relative to the peat surface were taken manually weekly throughout the growing season using wells established in the peat surface. Active layer depth was determined as the seasonal maximum thaw depth, where seasonal thaw depth was determined weekly using a tile probe driven into the peat surface in at least 6 spatially distinct regions of a plot on a given sample day.

SPECIES COMPOSITION

Plant species composition was estimated using the point frame method (Hollingsworth et al., 2010, Jonasson, 1988) for calculating absolute abundance, during peak biomass at the end of July/early August. Point frame quadrats covered an area of 1 m^2, and represented a total of 20 point readings per quadrat, with multiple hits on vegetation with canopy height at each point. Absolute abundance for each species was

calculated as a ratio of the number of hits per 20 readings within a quadrat. Measurements were recorded at the fen site in 2007, with three quadrats per water table treatment, quadrats were placed to coincide with ongoing gas flux measurements at each plot, and gas flux collars were placed randomly within each plot. I repeated this design at the fen site in 2009 (n= 3) and measured species abundance in 2009 in the bog site with 4, 4 and 6 quadrats in the permafrost, old collapse and new collapse plots respectively.

Plants were identified to species with the exception of mosses and lichens, which were keyed to genus. Sedge species were identified following nomenclature by Tande and Lipkin (2003); all other vascular species were identified following Hultén (1968). Moss genera followed Seppelt et al. (2008). Species were classified into: (1) plant growth forms for living vascular plants: grass, sedge, tree, deciduous shrubs, evergreen shrubs, and herbaceous forbs; (2) growth forms for mosses: brown moss, feather moss and *Sphagnum* spp. *Sphagnum* refers to all species within the genus *Sphagnum*, feather moss refers to mosses growing in linearly branching patterns (*Hylocomium*, *Pleurozium*, and *Ptilium*) and brown moss refers to true mosses typically associated with rich fens (families Amblystegiaceae and Brachytheciaceae).; or (3) dead plant groups: coarse woody debris, fine woody debris, leaf litter and standing dead. All components of the dead plant group were excluded for composition analysis, but were included in biomass comparisons between plots.

Plant productivity

ABOVEGROUND OVERSTORY BIOMASS AND NPP

There were no trees at the fen; however, at the bog I measured *Picea mariana* biomass, the only tree species present with individuals above breast height. Seedlings and standing dead were present in low density in the new and old collapse formations, and living trees were present in the permafrost plot. Diameter at breast height (DBH) was measured for all standing dead in the collapse scar plots, and all trees above DBH within a 600 m^2 area of the permafrost plot. Trees were recorded as either dead or living in October 2010, and biomass estimates were calculated using allometric equations from the

125 year old mesic black spruce stand of Mack et al. (2008). For the permafrost plot, new growth estimates for the overstory involved adding biomass from new branches and new leaves using the associated allometric equations. NPP was averaged by tree, and then scaled to the plot area level using tree density.

ABOVEGROUND UNDERSTORY BIOMASS AND VASCULAR NPP

Biomass samples were collected concurrently with point frame quadrats in 100 cm^2 subplots, collected at random along three transects (6-7 samples per transect) every 2-3 meters within a given plot, or immediately adjacent to a point frame quadrat (placed randomly within each plot). All aboveground understory biomass included within the area of the subplot was harvested for a sample, with the moss layer removed to the base of living moss in the peat surface layer. Samples were collected at peak biomass within a collection period of seven days for all plots at both sites. At the bog 24 samples were collected in the permafrost and old collapse plots and 26 samples were collected in the new collapse. At the fen 14 samples were collected in and around the control treatment plot and three samples were collected in each of the lowered and raised water table treatments due to limitations of destructive harvests within ongoing manipulation areas.

All biomass samples were initially separated into individual vascular plant species, moss growth forms, litter or woody debris. Vascular plant specimens were further subdivided into year of growth (new, living or dead). Living tissue referred to material that had not grown this previous summer, but was alive and functioning as part of the organism. Dead material that could be identified to the species level that was no longer living was designated as the category standing dead, while litter was the category reserved for remaining unknown dead material (Shaver and Chapin, 1991).

Aboveground net primary production (ANPP) for vascular species was determined by summing all designated new growth from the biomass harvest for each species, including leaves, stem and fruit (Mack et al., 2008, Shaver and Chapin, 1991) within each sample and calculating an average total biomass (m^2) for each plot. Secondary growth for shrubs was not measured, and therefore my measurements of

ANPP underestimate shrub NPP, however differences in secondary growth were likely several orders of magnitude lower than the effect of differences in abundance for each shrub species contributing to total plot biomass. ANPP for each plant growth form was determined by summing all species within a group by individual sample and calculated a mean ANPP (m^2) for each plot. All materials were weighed to 0.001 g using a PG 503-S Meller Toledo balance.

NON-VASCULAR NPP

Non-vascular productivity was measured using cranked wires in pure patches of different moss types (*Sphagnum*, feather moss, brown moss and *Dicranum*) in 2009 and 2010 (Clymo, 1970) to quantify linear growth. Pure patch estimates of moss NPP were scaled according to abundance cover estimates in g / m^2 to compare with other community function measurements. Linear growth of *Sphagnum* and feather moss was measured as a change in vertical length of cranked wires inserted into the peat surface as moss grew up around the wires (Clymo, 1970). Cranked wire arrays within a patch included 25 individual wires within the same moss type organized in to 5 rows of 5 columns spaced approximately 5 cm apart. Arrays were replicated for each dominant moss type present in my quadrats, and placed in pure patches accessible without disturbance to the peat surface along a lengthwise transect within each plot. Arrays were placed in different locations within both the fen and the bog between sampling years.

At the bog, I installed three *Sphagnum* arrays in each plot (only two in the old collapse plot) in 2009. In 2010, I installed three *Sphagnum* arrays in each plot. At the fen, I installed three *Sphagnum* arrays in the control plot but only one array in the lowered and raised plots due to limitations of peat disturbance in areas of ongoing manipulation. I converted linear growth rates (cm / yr) into biomass accrual per area (g / m^2 / yr) using surface bulk density measurements calculated from 125 cm^3 volume samples of *Sphagnum* moss collected from the same microhabitat. Capitula were removed from each stem before determining bulk density, as capitula mass was assumed to stay constant during the growing season (Benscoter, 2007; Thormann and Bayley, 1997). Bulk density

samples were collected in the fall of 2010 and were used to calculate NPP from the 2009 and 2010 linear growth rates. Due to differences in deployment times for the cranked wires between years, annual estimates of NPP were standardized by the number of days the wires were in place, and multiplied by 123 as the approximate length of the growing season. I averaged rates of NPP values (g / cm^2 / yr) across arrays within each moss type and scaled the values to a m^2 basis using moss type abundance data for each plot.

Feather moss linear growth rates were measured at the permafrost plot in the bog using cranked wires in 2009 (three arrays). My feather moss cranked wires were disturbed by wildlife in 2010. For this study, feather moss NPP was assumed to remain constant between 2009 and 2010. Conversion from linear growth rate to biomass accrual relied on cranked wire length measurements, individual stem density, and a horizontal growth parameter developed by Benscoter and Vitt (2007). NPP values were standardized to 123 growing days as described above.

Linear growth rates for brown moss cannot be accurately quantified using the cranked wire approach due to substantial horizontal growth on previous year growth. Therefore, brown moss NPP estimates were based upon values reported by Szumigalski and Bayley, 1996; Thormann and Bayley, 1997; Thormann et al., 1998, for estimated brown moss NPP in rich fens in Alberta, Canada (**Table 2.1**). New growth for *Dicranum* spp. was determined visually, based upon the color and width of the individual stem, with a distinct narrowing evident for the start of each new year's growth. New growth sections were removed and weighed for a known density of stems.

Measurements of moss NPP at the fen site were complicated by the above-surface water table position for the initiation of the measurement period (2009), and then drought conditions with the water table more than 30 cm below the surface throughout most of 2010. Consequently, these estimates must be approached cautiously for comparison with other sites and in more climatically average years.

BELOWGROUND VASCULAR NPP

I measured belowground NPP (BNPP) using root in-growth bags (diameter of approximately 6 cm, length ranging from 20-50 cm deep). Bags were constructed from nylon netting (1.5 cm opening size) and homogenized root-free surface peat from a local collapse scar. In-growth bags were installed in late September 2009 to limit surface disturbance during installation and were inserted into pre-drilled holes in the surface peat such that the top of the bag was flush with the microform surface. I installed 5 bags at the new and old collapse plots and 2 in the permafrost plot in the bog. At the fen, I installed 4, 2, and 2 in-growth bags at the control, lowered and raised plots, with reduced installation in the lowered and raised plots associated with minimizing disturbance in areas with ongoing manipulation and data collection.

Bags were removed in late September 2010, just after the upper peat surface began to freeze. In-growth bags were removed from the ground with residual peat surrounding them to prevent loss of roots via unintentional interruption in the core removal process. After removal of extra roots and peat outside the bags, the root in-growth bags were measured for exact length and diameter, and used to convert total root mass per core to root density. Densities were multiplied by the total length of each core to calculate BNPP ($g / m^2 / yr$).

VASCULAR GREEN AREA

I quantified seasonal changes in vascular green area (VGA, expressed as m^2 of leaf area / m^2) among species, sites and plots. Leaf area measurements of dominant species were conducted every two weeks throughout the growing season to calculate seasonal changes in photosynthetic surface area. For the first three leaf area measurements in 2009, I quantified lengths and widths for all leaves using a caliper on three individuals of each dominant species within a plot. Leaf area calculations were based upon geometric equations for leaf shape approximations (Chivers et al., 2009; Wilson et al., 2007). In 2009, these non destructive measurements were compared to a destructive approach, whereby I harvested three to five individuals for each species

within each plot during three sampling dates. The harvested specimens were measured for surface area by scanning all leaves with a LI-3000C Portable Leaf Area Meter (LI-COR, Lincoln, Nebraska). In 2010 all leaf area measurements were calculated using destructive harvest of three individuals per dominant species within a plot followed by measurement of leaf area using the LI-3000C.

Stem density for each dominant species per m^2 within a plot was measured approximately once per month during the growing season. Stem density estimates were calculated for five replicate samples (7.5 cm x 7.5 cm) within subplots nested within each plot. I established three subplots in each water table treatment at the fen. In 2009 I established 12, 6, and 6 subplots at the new collapse, old collapse and permafrost plots respectively. In 2010, I used 9, 6, and 6 subplots in the new collapse, old collapse and permafrost plots, respectively.

Leaf area for each species was multiplied by the number of individuals/area for measurements collected approximately every two weeks at each plot to produce the VGA for each species at a given time. Total VGA for a given sampling day was then calculated as the sum of all species present within the subplot. Plot average daily VGA was modeled using Proc NLIN in SAS 9.1 to model the seasonal change in total vascular green area per plot over time. Following Equation 1, I estimated maximum VGA (VGA_{max}), the day of year associated with maximum VGA (x_{max}), and the shape of the seasonal curve (b) (Wilson et al., 2007):

Equation 1 $\frac{}{}$

Data analysis

PROCESSING ENVIRONMENTAL VARIABLES

To correlate environmental variables (water table position and soil temperature) with plant species composition, I used mean growing season (April through October) and mean annual environmental data for each plot at the bog (2009 data only) and fen (2007 and 2009 data). Additionally, I calculated a coefficient of variance (CV) for each

environmental variable. If necessary, gap filling was performed for variables where one plot was missing a single variable and the cell could be filled using a regression relationship with other existing data. In such cases, the CV for that variable was then estimated using an average of associated plots for the same average variable. This process was required only for soil temperature at 10 cm depth for the lowered water table treatment at the fen. I used standardized Principal Components Analysis (PCA) to examine patterns in environmental variables across plots within each site. All variables with a 1st principal component loading of less than 0.001 were removed and the PCA was reanalyzed. Variables at the bog with the first PC less than 0.001 included the covariance of annual air temperature, and therefore this predictor was removed from further analysis. No variables at the fen had a PC 1 of less than 0.001.

The remaining variables were used as a secondary matrix for plant species composition data sets. Vectors of environmental variable correlations to a plant species composition matrix and non-metric axes were calculated using non-metric dimensional scaling (NMDS) ordination in PC ORD 5.31.

SPECIES DIVERSITY

I calculated plant diversity indices to examine differences in species and growth form composition between plots within each site. Species richness, alpha diversity or D_0, was measured as average quadrat level species richness within a plot, and species evenness (D_1) was calculated to determine the number of species of equal abundance (McCune & Grace, 2002). Comparison of species richness between plots at each site was conducted using ANOVA models, followed by Tukey post hoc tests. I calculated plot-level beta diversity, or the compositional change between quadrats, using the Whittaker beta diversity indices (β_w: McCune and Grace, 2002). Gamma diversity at the site level was the total number of species across plots within a site.

ORDINATION OF PLANT SPECIES COMPOSITION

I used non-metric dimensional scaling (NMDS) ordination (PCOrd 5.3, MjM software) to analyze patterns in plant species composition between plots within each site. NMDS ordination was selected due to the non-normal distribution of multivariate abundance data, and because I was interested in examining relationships between plots and specific species of vegetation that are most closely associated with each different plot (Hollingsworth et al., 2010). Dimensionality was assessed by comparing the stress levels associated with both real (50 runs) and randomized data (50 runs), and selecting the minimum number of axes that meet the criterion of maximum stress and a stability criterion of 0.00001. A relativization by maximum adjustment, to reduce the column variance associated with differences in species abundance, was applied to the bog species abundance data, while a weighting by ubiquity relativization was applied to the fen data.

The relative contributions of individual species to the overall variation and placement of plots within the ordination space were calculated using ordination loadings and plotted in the ordination space. Pearson correlations between each species and the ordination axes were used to examine compositional gradients across all plots. Environmental data collected at each plot were included as a vector component associated with each axis.

I used a Multi-response Permutation Procedures (MRPP) hypothesis test using Sørensen distances to test for significant differences in plant species and growth form group composition between plots within each site, as well as between years at the fen only. This test is a nonparametric method for determining whether there is a difference between two or more groupings of sample units (Clarke, 1993).

ANALYSIS OF PLANT BIOMASS AND PRODUCTIVITY

All analyses were performed using R v2.9.0 statistical programming language (R Development Core, 2009). To examine the effect of plot (i.e., water table manipulation at the fen or permafrost thaw at the bog) on ANPP, I analyzed data within each site using an ANOVA model followed by Tukey post hoc tests. Plot was included as a fixed effect.

Aboveground understory biomass data were log-transformed as the data were not normally distributed; log transformation appeared to correct the non-normal variance. For the fen data, only sample units paired with point frame units were used in plot comparisons to maintain a balanced design (n = 3). I used MANOVA models to examine how plant growth forms contributed to aboveground understory biomass and NPP within each plot at each site. Belowground NPP (BNPP) data were square root transformed due to non-normal variance; this transformation appeared to correct the non normality. An ANOVA model was used to analyze the effects of plot on BNPP within each site, using a forced balanced design with plot mean values filling in empty cells.

To determine the relationships among composition, biomass and ANPP data I calculated mean percent abundance, biomass and productivity for each species within each plot. These data were then used in ANCOVA tests with regressions between abundance and ANPP and between abundance and biomass to examine the potential for differences in slope and intercept between plots within a site. ANPP was treated as a dependent variable and required a square root transformation to correct non-constant variance. The abundance and biomass comparison used biomass as the dependent variable and also required a square root transformation to correct non-constant variance. All transformations successfully corrected issues of non-constant variance.

IV. Results

Effects of permafrost thaw in a bog

CLIMATE AND ENVIRONMENTAL VARIABLES

Results of a Principal Components Analysis (PCA-centered) of water table and temperature data differentiated between the permafrost plot and the collapse plots at the bog (**Figure 2.1A**). The first and second component axes accounted for 99% of the variance in environmental data (Axis 1: 95%; Axis 2: 4%). The first principle component (Axis 1) clearly separated the permafrost plot from both collapsed plots and was positively correlated with mean growing season water table position. Variance in annual soil temperature at 25 cm depth was the second most important contributor (0.30) to Axis

1. The second axis (Axis 2) separated the new and old collapse plots, and was negatively correlated with the mean growing season soil temperature at 2 cm depth (-0.48), covariance of the water table (-0.47), and growing season soil temperature at 10 cm (-0.43).

PLANT SPECIES COMPOSITION AND BIOMASS

Species turnover between plots was fairly high, with only 5 of 19 species present at all three plots (**Table 2.2**; *Andromeda polifolia*, *Chamaedaphne calyculata*, *Oxycoccus microcarpus*, and trace amounts of *Larix laricina* and *Betula glandulosa*). Conversely, 9 of 12 species were common to both collapse plots. *Carex aquatilis*, *Potentilla palustris*, and *Eriophorum chamissonis* were present in both collapse plots, but were absent in the permafrost plot. *Eleocharis palustris* was only found in the old collapse plot, *Equisetum arvense* was present in both the old collapse and the permafrost plot, while *Ledum decumbens* and *Picea mariana* were present in the permafrost plot and large hummocks of the new collapse. Species present only in the permafrost plot included *Calamagrostis canadensis*, *Eriophorum vaginatum*, *Peltigera apthosa*, *Rubus chamaemorus*, *Vaccinium uliginosum*, and *V. vitis-idaea*. Species richness varied among the bog plots ($F_{2, 11} = 7.93$, $p = 0.007$), and was greatest in the permafrost plot (**Table 2.3**). Species evenness also varied among plots, and was highest in the permafrost plot ($F_{2, 11} = 20.82$, $p = 0.0002$; **Table 2.3**). The change in composition between quadrats within a plot (B_w) was higher in the collapse plots than in the permafrost plot (**Table 2.3**).

A MRPP test showed that the bog plots were significantly different in plant species composition ($A = 0.271$; $p = 0.0002$). The permafrost plot differed from both the new ($A = 0.334$; $p = 0.0013$) and old collapse ($A = 0.250$; $p = 0.0059$), while there were no differences among the collapse plots ($A = 0.059$; $p = 0.054$).

Plant species abundance at the bog produced a two dimensional NMDS ordination plot (**Figure 2.2A**). Approximately 90% of variance in plant species abundance was associated with Axis 1 and 2 (Axis 1: 29%, Axis 2: 61%), and numerous species showed strong correlations with either or both axes that contributed to spatial separation of each

plot (**Table 2.4**). Pearson correlations between environmental variables and the NMDS axes indicate that Axis 1 was strongly correlated with changes in mean growing season water table position ($R^2 = 0.60$) and deeper soil temperature across plots ($R^2 = 0.63$), while Axis 2 was strongly correlated with mean growing season water table position ($R^2 = 0.92$), mean annual air temperature ($R^2 = 0.90$), and mean growing season air temperature across plots ($R^2 = 0.90$) (**Figure 2.2B**). Both of these gradients clearly separated the permafrost plot, which in general has cold, dry surface peat, from the wetter collapse plots. However, differences in water table position and deeper soil temperatures also helped to differentiate between the old and new collapse plots. The old collapse had a lower seasonal average water table position and warmer soil temperatures at 10 and 25 cm depth compared to the new collapse plot.

There were significant differences in total understory aboveground biomass between the bog plots ($F_{2,70} = 4.97$, $p = 0.0096$). The permafrost plot had more aboveground understory biomass (869 ± 78 g / m^2) compared to the new (663 ± 40 g / m^2) and old (591 ± 60 g / m^2) collapse plots. There were also significant differences in the biomass of different growth forms across plots (**Figure 2.3A**; MANOVA, $F_{2,18} = 2.82$, $p < 0.0007$). In general, the collapse plots had lower biomass of evergreen shrubs ($F_{2, 70} = 7.17$, $p = 0.0015$) and debris ($F_{2, 70} = 10.52$, $p = 0.0001$) than the permafrost plot.

There were no live trees in either collapse plot. Standing dead tree biomass was 103.2 ± 11 g / m^2 in the new collapse, and 10.9 g / m^2 the old collapse. The permafrost plot contained 9.1 ± 1 g / m^2 standing dead biomass and 141.5 ± 13 g / m^2 of living tree biomass.

PLANT PRODUCTIVITY

Moss NPP varied among the three bog plots and was highest in the new collapse and lowest in the old collapse plot (**Table 2.5**). There were no differences in total understory vascular ANPP among plots ($F_{2, 70} = 0.55$, $p = 0.581$; **Table 2.6**). These aboveground values likely underestimate ANPP in the permafrost plot as they do not include estimates of ANPP for vegetation between 1 and 1.37 m (i.e. trees shorter than

breast height yet not short enough to have been measured using understory methods). Sedge ANPP varied among plots ($F_{2, 70} = 15.04$, $p < 0.00001$) and was higher in the new collapse than in the other plots. Evergreen shrub ANPP also varied among plots ($F_{2, 70} = 5.24$, $p = 0.0076$; **Figure 2.3B**) and was higher in the permafrost plot than either collapse plots. Belowground NPP (BNPP) also varied among bog plots ($F_{2, 12} = 22.71$, $p < 0.0001$) and was lower in the new collapse relative to the permafrost and old collapse plots (**Table 2.6**).

There were differences in VGA_{max}, and in the timing of VGA_{max} (X_{max}) across plots. The permafrost plot had the highest VGA_{max}, in addition to the earliest X_{max} in 2010 relative to the collapse plots (**Table 2.7**). However the VGA model did not converge at the permafrost plot using 2009 data due to an exponential rather than a quadratic pattern between sampling dates in late season VGA measurements. The new collapse plot had intermediate VGA_{max} and the latest X_{max} in both 2009 and 2010 relative to the other plots. Across plots, VGA_{max} was lower and X_{max} was delayed in 2010 relative to 2009.

THE EFFECTS OF PLANT SPECIES ABUNDANCE ON ANPP AND BIOMASS

Analysis of covariance showed that the relationship between understory aboveground abundance (% cover) and square root transformed understory biomass varied among plots, with a significant biomass x plot interaction (**Figure 2.4A**; $F_{2\ 1} = 4.7$, $p = 0.013$). Individual regressions for each plot (**Table 2.8**) showed that the slopes of the abundance-biomass relationships were comparable between the old and new collapse plots, but were steeper for the permafrost plot. This indicates that similar increases in plant cover led to higher levels of biomass in the permafrost plot relative to the collapse plots. Similar to the biomass relationship, analysis of covariance also showed that the relationship between species abundance and square root transformed ANPP varied among plots (**Figure 2.4B**; ANPP x plot interaction: $F_{2\ 1} = 6.5$, $p = 0.004$). Individual regressions for each plot showed similar slopes for the permafrost and new collapse plots but a steeper slope at the old collapse plot (**Table 2.8**).

Effects of water table manipulation in a fen

CLIMATE AND ENVIRONMENTAL VARIABLES

A PCA clearly separated the water table manipulation plots at the rich fen based on environmental data (water table, and soil temperature data at 0 cm, 2 cm, 10 cm, and 25 cm below ground surface) collected in 2007, however, all the 2009 data were spatially located together in the ordination space (**Figure 2.1B**). The first and second component axes explained 92% in environmental data (Axis 1: 57%; Axis 2: 36%).The first axis separated the raised plot from the control and lowered for data collected in 2007 only, and was negatively correlated with the covariance of annual air temperature (-0.79) as well as the covariance of growing season soil temperature at 10 cm depth (-0.58). The second axis separated data from 2007 and 2009, and was positively correlated with annual covariance of soil temperature at 10 cm depth (0.71), while also being negatively associated with annual air temperature (-0.59).

To determine whether there were differences between plots in 2009 environmental data at the fen plots, I ran a second PCA ordination using data only from 2009 (**Figure 2.1C**). The first two principle components explained 100% (Axis 1: 86%, Axis 2: 14%) of the total variance in environmental variables between plots. This analysis differed from the PCA using all environmental data, as it did a better job separating treatment plots. Axis 1 separated the raised plot from the control and lowered plots and was positively correlated with mean growing season water table position. Axis 2 separated the lowered water table plot from the control plot, and was positively correlated with mean annual and mean growing season soil temperature at 25 cm.

PLANT SPECIES COMPOSITION AND BIOMASS

At the fen I identified 8 plant species, three of which were found in each water table plot in high abundance (**Table 2.2**). Two species were found only in the raised plot (*Carex lasiocarpa* and *Galium trifidum*), and three species were found in two of the three plots (*Calamagrostis canadensis*- lowered and raised, *C. canescens*- control and raised, and *Potamogeton gramineus*- control and raised). The raised plot had significantly higher

species richness than the control or lowered plot (ANOVA; $F_{2, 6} = 14$, $p = 0.005$), while the lowered plot contained the lowest average number of species (**Table 2.3**). There was no difference in species evenness between plots. Despite having a lower number of plant species, the lowered plot had the highest beta diversity between quadrats, suggesting that the few species present in this plot were more clumped than species in the other plots.

Overall, there were significant differences in species abundance between water table treatments based upon a MRPP test ($A = 0.208$; $p < 0.0001$). The control plot had higher brown moss and lower *C. atherodes* abundance making it compositionally different from both the lowered ($A = 0.250$, $p = 0.0005$) and raised ($A = 0.117$, $p = 0.0099$). The lowered plot showed reduced brown moss relative to the raised plot and therefore species composition varied between these plots ($A = 0.125$, $p = 0.0067$). Composition varied by a plot x year interaction (2007 vs. 2009) with greater abundance of *C. atherodes* and *Sphagnum* in the control plot in 2009 ($A= 0.235$, $p = 0.0234$). The lowered and raised plots did not appear to have significant differences in species composition among years.

Three major axes in a NMDS ordination captured 95% of the variance in species composition between water table treatments at the fen (Axis 1: 15%, Axis 2: 35%, Axis 3: 46%; **Figure 2.5A**). Environmental gradients associated with each axis showed that Axis 1 was most closely correlated positively to growing season surface temperature ($R^2 = 0.2$), Axis 2 was positively correlated to water table position ($R^2 = 0.42$) and soil temperature at 25 cm ($R^2 = 0.50$), and Axis 3 was negatively correlated the variation of growing season surface soil temperatures ($R^2 = 0.33$) (**Figure 2.5B**). The abundance of certain plant species also were correlated with the NMDS axes (**Table 2.9**) In particular *C. atherodes* was positively correlated with Axis 1, while *Sphagnum* was positively correlated with Axis 2, and brown moss was positively correlated with Axis 3.

There were no significant differences in aboveground vascular biomass among the water table plots including total biomass ($F_{2, 6} = 3.46$, $p = 0.1000$) as well as biomass among individual plant growth forms (MANOVA; $F_{2, 14} = 0.93$, $p = 0.5$; **Figure 2.6A**).

While this trend was not significant, there was slightly higher aboveground vascular biomass in the lowered plot relative to the other plots.

PLANT PRODUCTIVITY

Total moss NPP, scaled by the abundance of each moss type, was highest at the control plot and lowest at the lowered plot (**Table 2.6**). Rates of NPP specific for each functional group are reported by year in **Table 2.5.** *Sphagnum* NPP was highest in the raised plot, and lowest in the lowered plot. There were no differences in BNPP ($F_{2,9}$ = 0.21, p = 0.813; **Table 2.6**), vascular ANPP ($F_{2,6}$ = 1.03, p = 0.4113), nor individual plant growth form contributions to total ANPP (MANOVA Pillai test; $F_{2,17}$ = 1.11, p = 0.3872; **Figure 2.6B**) among the three water table plots. Maximum seasonal VGA (VGA_{max}) varied among study years (2009 vs. 2010) and water table plots (**Table 2.6**). In general, VGA_{max} tended to be greater in the lowered plot than in the other plots. X_{max} tended to be earlier in 2009 than in 2010 although there was no clear pattern among plots.

THE EFFECTS OF PLANT SPECIES ABUNDANCE ON ANPP AND BIOMASS

Analysis of covariance results showed that slopes of the relationship between plant species abundance (% cover estimates) and square root transformed understory biomass did not vary among treatment plots (**Figure 2.7A**; $F_{2\,1}$ = 0.79, p = 0.470). However, intercept terms for these relationships did vary among plots ($F_{2\,1}$= 7.41, p = 0.013), with a greater intercept for the control plot relative to the lowered or raised plots. ANCOVA results showed that the relationships between species abundance and square root transformed ANPP varied among plots (**Figure 2.7B**; **Table 2.8**; $F_{2\,1}$ = 5.96, p = 0.016), with a steeper slope in the lowered plot relative to the control and raised plots.

V. Discussion

Response of vegetation to permafrost thaw in a boreal bog

Permafrost thaw and the development of collapse scars in peatlands have increased landscape scale species richness by as much as 47% (Beilman, 2001), as the

creation of novel microforms and soil environmental conditions in peatlands provides habitat for specialist species. At the landscape scale, my results support this trend for vascular species, with collapse scar formation increasing overall bog diversity by 27%. At the scale, of plot level ecosystem differences however, species diversity is generally higher before permafrost thaw (Luken, 1984), as collapse scar bogs typically are *Sphagnum* dominated and have lower species diversity (Beilman, 2001). My results showed that within the collapse scars there was a 58% decrease in species diversity relative to the permafrost plateau, suggesting that as collapsed areas become more widespread in the floodplain there will be a loss in species diversity with the transition to a more aquatic ecosystem.

Comparisons between Canadian peat plateau bogs and adjacent collapse scars have shown that changes in water table have a substantial influence on plant community composition (Beilman, 2001; Camill, 1999). My study confirms the importance of water table position as a control on species composition. The water table of the permafrost plot was limited by the thaw depth, yet by the end of the growing season far exceeded the water table of collapse plots. Compositionally the permafrost plot supported feather mosses, and a range of deciduous and evergreen shrubs (e.g. *Vaccinium vitis-idaea*) that were only present in low densities on large hummocks within the collapse formations, or were absent altogether. Further, the average growing season water table was highly correlated with the main multivariate axis associated with separating the permafrost plot from the collapse formations.

My results also highlight the influence of soil temperature on peatland vegetation. Colder soil temperatures in the peat plateau likely slow decomposition, limit the rooting zone and may reduce the rates of nutrient cycling relative to the warmer collapse scar formations. This may be especially important for deeper rooted sedge species that are absent from hollows within the permafrost plot and present in high abundance in the collapse formations (e.g. *Carex aquatilis* and *Eriophorum chamissonis*). Differences in temperature between the permafrost plateau and the collapse formations is further complicated by interactive feedbacks between the permafrost presence and supporting

moss layer, which may in fact act as a buffer maintaining the permafrost (and therefore soil temperatures) at cold temperatures (O'Donnell et al., 2009). Differences in moss composition may also play into the temperature differences between the peat plateau and collapse scar continuation.

Between the old and new collapse scars there were differences in soil temperature and water table variation. The old collapse plot had cooler soil temperatures and less variation in water table position relative to the new collapse plot. Compositionally the old collapse contained more deciduous shrubs, namely *Betula glandulosa*, and included a comparatively greater abundance of *Oxycoccus microcarpus* (bog cranberry). Both of these species grew on small hummocks of *Sphagnum papillosum* and *S. fuscum*, which were only 3-10 cm above the water table, and therefore likely benefiting from a reduction in variability of distance to water table position.

Previous studies have found that permafrost thaw reduces plant biomass, as biomass is generally higher in forested peat plateaus than in un-forested collapse scars (Camill et al., 2001; Luken, 1984). My results are similar: I found that biomass averaged 999 ± 79 g/m^2 in the peat plateau and 727 ± 37 g/m^2 in the two collapse scars. The effects of permafrost thaw on NPP in previous studies have been less consistent. Some studies have shown no change in NPP with permafrost thaw, as increases in moss NPP post-thaw compensates for decreases in tree NPP (Camill et al., 2001). Other studies, however, have measured increased rates of peat accumulation following permafrost thaw and have implied that this is a result of greater NPP in the collapse scars (Turetsky et al., 2007; Turetsky et al., 2010). Overall, I found no difference in total ANPP between the permafrost and collapse plots. However, my results showed a 30% increase in moss NPP and a 67% decrease in total vascular NPP with permafrost thaw (permafrost plot compared to the new collapse plot). I also quantified VGA across plots, and found that understory VGA decreased following permafrost thaw. Because total ANPP was constant or slightly increased following permafrost thaw, this trend in VGA suggests that mosses were the primary contributor to productivity in the collapse plots.

To my knowledge, no studies have measured belowground NPP (BNPP) in peatlands influenced by permafrost thaw. I expected that declines in woody vegetation with permafrost thaw would result in lower BNPP. My results partially support this prediction, as BNPP was lower in the new collapse plot than in the permafrost plot. However, there was no difference in BNPP between the permafrost and old collapse plots.

Peatland succession following permafrost thaw

While several studies have used paleoecological approaches to examine changes in plant community composition over time in areas affected by permafrost thaw (Beilman, 2001; Kuhry et al., 1993), no studies to my knowledge have used a space for time substitution (i.e. chronosequence) to examine peatland succession following permafrost thaw. My study was not designed to examine successional trends post-thaw, though the different timing of permafrost thaw in the two collapse plots (new collapse thawed 25 years prior and the old collapse thawed 45 years prior) allows for some insights into successional processes. Total biomass and components of NPP differed between collapse plots, with higher biomass and lower BNPP in the new collapse plot, whereas understory vascular biomass was similar between the two collapse plots. Standing dead biomass associated with *P. mariana*, however, was much lower in the old collapse than in the new collapse. This result is not surprising as previous work has shown that standing snags topple at some point post-permafrost thaw, and are buried by accumulating moss layers. If this dead woody debris was buried, this input of recalcitrant carbon to the soil could have important implications for decomposition and peat accumulation rates (Manies et al., 2004). Finally, moss NPP was higher in the new collapse than in the old collapse, which was expected due to a less variable and higher water table in the new collapse.

While there was no difference in vascular ANPP between the two collapse plots, BNPP was significantly higher in the old collapse relative to the new collapse plot. This suggests that succession after permafrost thaw influenced belowground more than

aboveground productivity. When considering individual plant growth form contributions to ANPP and aboveground biomass, the new collapse had more sedges and less deciduous shrubs than the old collapse plot.

I found that the relationships between species abundance, biomass, and ANPP varied among plots. Thus, while succession both during and after permafrost thaw resulted in changes in plant group contributions to productivity and biomass, this also likely led to changing functional relationships between plant abundance and biomass production. For example, I found that similar levels of plant abundance were associated with greater amounts of aboveground biomass in the permafrost plot relative to the collapse plots. This increase in slope was likely driven by the presence of *Ledum decumbens* and *V. uliginosum*. On the other hand, similar levels of species abundance were associated with greater ANPP in the old collapse plot relative to the permafrost or the new collapse plot. The species that appear to drive this difference are the evergreen shrub *Andromeda polifolia*, which is less present in the old collapse and absent in the permafrost plot, *Betula glandulosa* and seedlings of *Larix laricina*. While all of these species are present in the new collapse, it appears that these species become more prevalent with collapse scar succession, and tend to co-inhabit similar low forming hummocks within the older collapse.

Response of vegetation dynamics to water table position manipulation in a fen

Long term draining experiments in fens have shown rapid succession from moss and sedge dominated systems to shrub and mature tree dominated peatlands within 55 years (Laine et al., 1995). Shorter term manipulation experiments have supported rapid changes in the moss layer associated with a decrease in the water table position, and increases in moss productivity with an increase in water availability (Thormann et al., 1998; Weltzin et al., 2000). Natural variation in water table position has additionally prompted vegetation functional responses to water table position frequently in terms of carbon uptake and rates of new growth (Moore et al., 2002).

In my study vegetation response to five years of flooding showed a significant change in species composition, with an increase in species richness associated with sedge species. Simultaneously in the drained plot there was a reduction in vascular species richness, as sedge species were lost during the 5 years of manipulation. Despite compositional differences between manipulation plots, my results show no differences in total aboveground biomass among plots. This could be due to the relatively short period of time since manipulation. Many other studies have found differences in biomass with varying water table position (Moore et al., 2002; Murphy et al., 2009; Weltzin et al., 2000) however most observed changes were related to differences in compositional abundance between major functional groups and especially the growth of trees (Laine et al., 1995). The site studied here is an open moderate rich fen that lacks shrub diversity (only one aquatic species) and contains no trees. This obviously limits the potential for increased woody biomass with decreased water table depth.

I explored the effects of water table manipulations on above and below-ground productivity and seasonal changes in vascular green area. The lowered plot consistently had greater VGA in both 2009 and 2010 relative to the other plots. Vascular NPP was also greatest in the lowered plot, with no differences in NPP between the control and raised plots. Below-ground productivity is often predicted to track aboveground productivity (Moore et al., 2002; Murphy et al., 2009). However, my results showed no difference in BNPP between plots. My increase in vascular NPP in the lowered plot wasn't significant, and the trend was closely associated with the increase in size of the deciduous shrub *Potentilla palustris*. This species showed high variation in biomass, and in spatial abundance throughout the plot, thereby potentially limiting an effect on measurable BNPP.

While the lowered plot had greater vascular productivity, at least aboveground, moss productivity was greatest in the control plot and smallest in the lowered plot. None of these trends were significant, however these results do support the hypothesis that net ecosystem productivity (NEP) would be resilient to fluctuations in water table within this fen system, associated with tradeoff between aboveground vascular and non-vascular

growth (Turetsky et al., 2010). Directional trends may be more difficult to predict, as species introductions of shrub or tree species would allow accumulation of woody tissues in the peat layer that may increase rates of peat accumulation. Alternatively permanent flooding may favor obligate wetland species with little structural tissue and NEP may become controlled not by plant species but by algae and dissolved organic carbon dynamics, which were not measured here.

In general it appears that drying conditions have created a greater change in vegetation dynamics than flooding in a five year water table manipulation experiment at a moderate rich fen in interior Alaska. Vegetation composition has varied in the raised (flooded) plot with an increase in the number of sedge species and increased species richness in general; however this appears to be the main effect. Additionally, the lowered (dry) plot showed a reduction in moss cover and species richness, an increase in vascular green area and an increase in above ground vascular NPP associated with the deciduous shrub *Potentilla palustris*. Continued monitoring of these plots may clarify these diverging trends and determine the time scale associated with plant community response to manipulations in water availability associated with *in situ* experimentation.

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VIII. Literature cited

Andrus, R. E. (1986). Some aspects of *Sphagnum* ecology. *Botany*, *64*(2), 416-426.

Beilman, D. W. (2001). Plant community and diversity change due to localized permafrost dynamics in bogs of western Canada. *Canadian Journal of Botany*, 79(8): 983-993.

Benscoter, B. W. (2007). PhD Thesis. Southern Illinois University-Carbondale.

Benscoter, B. W., & Vitt, D. H. (2007). Evaluating feathermoss growth: a challenge to traditional methods and implications for the boreal carbon budget. *Journal of Ecology*, *95*(1), 151-158.

Blodau, C. (2002). Carbon cycling in peatlands — A review of processes and controls. *Environmental Review*, *10(2)*, 111-134.

Camill, P. (1999). Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal Botany, 77(5)*, 721-733.

Camill, P., & Clark, J. S. (1998). Climate change disequilibrium of boreal permafrost peatlands caused by local processes. *The American Naturalist, 151(3),* 207-22.

Camill, P., Lynch, J. A., Clark, J. S., Adams, J. B., & Jordan, B. (2001). Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems*, *4(5),* 461-478.

Chapin, F. S., McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., Kasischke, E.S., Euskirchen, E. S., Jones, J. B., Jorgenson, M. T., Kielland, K., Kofinas, G. P., Turetsky, M. R., Yarie, J., Lloyd, A. H., & Taylor, D. L. (2010). Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research*, *40(7),* 1360-1370.

Chimner, R. A., & Cooper, D. J. (2003). Carbon dynamics of pristine and hydrologically modified fens in the southern Rocky Mountains. *Canadian Journal of Botany*, *81(5)*, 477-491.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2009). Effects of experimental water table and temperature manipulations on ecosystem CO_2 fluxes in an Alaskan rich fen. *Ecosystems*, *12(8)*, 1329-1342.

Clarke, K. (1993). Non-parametric multivariate analyses of changes in community structure. *Austral Journal of Ecology*, *18(1)*, 117–143.

Clymo, R. S. (1970). The growth of *Sphagnum*: methods of measurement. *The Journal of Ecology*, *58(1)*, 13-49.

Finer, L., & Laine, J. (2000). The ingrowth bag method in measuring root production on peatland sites. *Scandinavian Journal of Forest Research*, 15*(1)*, 75-80.

Hansen, J., Sato, M., Ruedy, R., Lo, K., Lea, D. W., & Medina-Elizade, M. (2006). Global temperature change. *Proceedings of the National Academy of Sciences of the United States of America*, *103(39)*, 14288-93.

Hinzman, L. D., Bettez, N. D., Bolton, W. R., Chapin, F. S., Dyurgerov, M. B., Fastie, C. L., Griffin, B., Hollister, R. D., Hope, A., Huntington, H. P., Jensen, A. M., Jia, G. J., Jorgenson, T., Kane, D. L., Klein, D. R., Kofinas, G., Lynch, A. H., Lloyd, A. H., McGuire, A. D., Nelson, F. E., Oechel, W. C., Osterkamp, T. E., Racine, C. H., Romonovsky, V. E., Stone, R. S., Stow, D. A., Sturm, M., Tweedie, C. E., Vourlitis, G. L., Walker, M. D., Walker, D. A., Webber, P. J., Welker, J. M., Winker, K. S., & Yoshikawa, K. (2005). Evidence and implications of recent climate change in northern Alaska and other arctic regions. *Climatic Change*, *72(3)*, 251-298.

Hinzman, L. D., Viereck, L. A., Adams, P. C., Romanovsky, V. E., & Yoshikawa, K. (2006). Climatic and permafrost dynamics of the Alaskan boreal forest. *Alaska's changing boreal forest* (pp. 0-34).

Hollingsworth, T. N., Lloyd, A. H., Nossov, D. R., Ruess, R. W., Charlton, B. A., & Kielland, K. (2010). Twenty-five years of vegetation change along a putative successional chronosequence on the Tanana River, Alaska. *Canadian Journal of Forest Research*, *40(7)*, 1273-1287.

Hultén, E . (1968). Flora of Alaska and neighboring territories. Stanford Press, Stanford, CA.

Jonasson, S. (1988). Evaluation of the point intercept method for the estimation of plant biomass. *Oikos*, *52(1),* 101.

Jorgenson, T. M., Racine, C. H., Walters, J. C., & Osterkamp, T. E. (2001). Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, *48(4)*, 551-579.

Jorgenson, T. M., Romanovsky, V., Harden, J., Shur, Y., O'Donnell, J., Schuur, E. A. G., Kanevskiy, M., & Marchenko, S. (2010). Resilience and vulnerability of permafrost to climate change. *Canadian Journal of Forest Research*, *40(7),* 1219-1236.

Kane, E. S., Turetsky, M. R., Harden, J. W., McGuire, A. D., & Waddington, J. M. (2010). Seasonal ice and hydrologic controls on dissolved organic carbon and nitrogen concentrations in a boreal-rich fen. *Journal of Geophysical Research*, *115*, 1-15.

Kuhry, P., Nicholson, B. J., Gignac, L. D., Vitt, D. H., & Bayley, S. E. (1993). Development of *Sphagnum*-dominated peatlands in boreal continental Canada. *Canadian Journal of Botany*, *71(1),* 10-22.

Laine, J., Silvola, J., Tolonen, K., Alm, J., Nykänen, H., Sallantaus, T.,Savolainen, I., Sinisalo, J., & Martikainen, P. J. (1996). Effect of water-level drawdown on global climatic warmings: northern peatlands. *Ambio*, *25(3),* 179-184.

Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *The Journal of Applied Ecology*, *32(4),* 785.

Luken, AJ O., & Billings, W.D. (1984). Changes in bryophyte production associated with a thermokarst erosion cycle in a subarctic bog. *Oikos*, *9(3),* 163-168.

Mack, M. C., Treseder, K. K., Manies, K. L., Harden, J. W., Schuur, E. A. G., Vogel, J. G., Randerson, J. T., & Chapin, F.S III. (2008). Recovery of aboveground plant biomass and productivity after fire in mesic and dry black spruce forests of interior Alaska. *Ecosystems*, *11(2),* 209-225.

Manies, K. L. Harden, J. W., Bond-Lamberty, B. P., & O'Neil, K. P. 2004. Woody debris along an upland chronosequence in boreal Manitoba and its impact on long-term carbon storage. *Canadian Journal of Forest Research*, *35(2),* 472-482.

McCune, B., & Grace, J. B. 2002. Analysis of ecological communities. MjM Software Design. Gleneden Beach, Oregon.

Moore, T. R., Bubier, J. L., Frolking, S. E., Lafleur, P. M., & Roulet, N. T. (2002). Plant biomass and production and CO_2 exchange in an ombrotrophic bog. *Journal of Ecology, 90(1),* 25-36.

Murphy, M., Laiho, R., & Moore, T. R. (2009). Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems, 12(8),* 1268-1282.

O'Donnell, J. A, Romanovsky, V. E., Harden, J. W., & McGuire, A D. (2009). The effect of moisture content on the thermal conductivity of moss and organic soil horizons from black spruce ecosystems in interior Alaska. *Soil Science, 174(12),* 646-651.

Osterkamp, T. E., Viereck, L., Shur, Y., Jorgenson, M. T., Racine, C. H., Doyle, A., & Boone, R. D. (2000). Observations of thermokarst and its impact on boreal forests in Alaska. *Arctic, Antarctic, and Alpine Research, 32(3),* 303-315.

Osterkamp, T. E., Jorgenson, M. T., Schuur, E. A. G., Shur, Y. L., Kanevskiy, M. Z., & Vogel, J. G. (2009). Physical and ecological changes associated with warming permafrost and thermokarst in interior Alaska. *Permafrost and Periglacial Processes, 20,* 235-256.

R Development Core Team (2009). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL http://www.R-project.org.

Riordan, B., Verbyla, D., & McGuire, A. D. (2006). Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research, 111*(G4).

Roach, J., Griffith, B., Verbyla, D., & Jones, J. (2011). Mechanisms influencing changes in lake area in Alaskan boreal forest. *Global Change Biology, 17(8),* 2567-2583.

Seppelt, R. D., Laursen, G. A., & Lichvar, R. W. (2008). A guide to Alaskan black spruce wetland bryophytes: species specific to delineation for interior and south central regions. US Army Corps of Engineers.

Shaver, G. R., & Chapin, F. S III. (1991). Production: biomass relationships and element cycling in contrasting arctic vegetation types. *Ecological Monographs*, *61(1),* 1-31.

Strack, M., & Waddington, J. M. (2007). Response of peatland carbon dioxide and methane fluxes to a water table drawdown experiment. *Global Biogeochemical Cycles*, *21(1),* 1-13.

Szumigalski, A. R., & Bayley, S. E. (1996). Net above-ground primary production along a bog-rich fen gradient in Central Alberta, Canada. *Wetlands*, *16(4),* 467-476.

Tande, G. & Lipkin, R. (2003). Wetland sedges of Alaska. Alaska Natural Heritage Program Environment and Natural Resources Institute. Anchorage, AK.

Thormann, M. N., & Bayley, S. E. (1997). Aboveground plant production and nutrient content of the vegetation in six peatlands in Alberta, Canada. *Plant Ecology 131(1)*, 1-16.

Thormann, M. N., Bayley, S. E., & Szumigalski, A. R. (1998). Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta: implications for global warming. *Hydrobiologia*, *362(1-3)*, 171-183.

Turetsky, M. R., Treat, C. C., Waldrop, M. P., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2008). Short-term response of methane fluxes and methanogen activity to water table and soil warming manipulations in an Alaskan peatland. *Journal of Geophysical Research*, *113*, G00A10.

Turetsky, M. R., Wieder, R. K., Vitt, D. H., Evans, R. J., & Scott, K. D. (2007). The disappearance of relict permafrost in boreal North America: effects on peatland carbon storage and fluxes. *Global Change Biology*, *13(9),* 1922-1934.

Turetsky, M. R., Mack, M. C., Hollingsworth, T. N., & Harden, J. W. (2010). The role of mosses in ecosystem succession and function in Alaska's boreal forest. *Canadian Journal of Forest Research*, *40(7),* 1237-1264.

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., & Harth, C. (2001). Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecological Applications*, *11(2),* 311-326.

Vitt, D. H., Halsey, L. A, Bauer, I. E., & Campbell, C. (2000). Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences*, *37(5),* 683-693.

Vitt, D. H. (2006). Functional Characteristics and Indicators of Boreal Peatlands. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal Peatland Ecosystems* (Vol. 188, pp. 9-24). Springer-Verlag Berlin Heidelberg.

Walsh, J. E., Chapman, W. L., Romanovsky, V., Christensen, J. H., & Stendel, M. (2008). Global Climate Model Performance over Alaska and Greenland. *Journal of Climate*, *21(23),* 6156-6174.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., & Chapin, C. T. (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, *81(12),* 3464-3478.

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K. A, Farrell, E. P., Tuitta, E.S. (2007). A high resolution green area index for modelling the seasonal dynamics of CO_2 exchange in peatland vascular plant communities. *Plant Ecology*, *190(1),* 37-51.

IX. Figures and Tables

Table 2.1. Brown moss NPP measurements as estimated for two boreal rich fens under natural variation in water availability (Alberta, CA) and manipulated water availability (Interior, AK).

Rich Fen in Alberta, CA°	Year	NPP (g/m^2)	Total summer precip	Difference from average summer precip.	WT
	1991	47	258.2	-25.0	8.0
	1992	38	235.0	-48.2	-8.0
	1993	25	433.8	150.6	-4.0
	1994	125	322.4	39.2	20.0
Rich Fen in interior, AK	**Year**	**NPP (g/m^2)**	**Total summer precip**	**Water table manipulation plot**	**WT**
	2009	47*	99.3	Control	12.0
	2009	47*	99.3	Lowered	13.7
	2009	47*	99.3	Raised	7.9
	2010	38*	119.4	Control	-25.0
	2010	25*	119.4	Lowered	-35.0
	2010	38*	119.4	Raised	-16.9

° Data from Szumigalski and SE. Bayley,1996; Thormann and Bayley, 1997; Thormann et al., 1998.
*Indicates NPP rates that relied on data from Thormann et al., 1998

Table 2.2. Plant species present in my two study sites along with growth form classification.

Species	Growth Form	Site
Andromeda polifolia	Evergreen shrub	Bog
Betula glandulosa	Deciduous shrub	Bog
Calamagrostis canadensis	Grass	Both
Carex aquatilis	Sedge	Bog
Carex atherodes	Sedge	Both
Carex canescens	Sedge	Fen
Carex lasiocarpa	Sedge	Fen
Chamaedaphne calyculata	Evergreen shrub	Bog
Drosera rotundifolia	Forb	Bog
Eleocharis palustris	Sedge	Bog
Equisetum arvense	Forb	Bog
Equisetum fluviatile	Forb	Fen
Eriophorum chamissonis	Sedge	Bog
Eriophorum vaginatum	Sedge	Bog
Galium trifidum	Forb	Fen
Larix laricina	Tree	Bog
Ledum decumbens	Evergreen shrub	Bog
Oxycoccus microcarpus	Forb	Bog
Picea mariana	Tree	Bog
Potamogeton gramineus	Forb	Fen
Potentilla palustris	Deciduous shrub	Both
Rubus chamaemorus	Forb	Bog
Salix sp	Deciduous shrub	Bog
Vaccinium uliginosum	Deciduous shrub	Bog
Vaccinium vitis-idaea	Evergreen shrub	Bog
	Sphagnum	Both
	Brown moss	Fen
	Feather moss	Bog
	Dicranum	Bog
	Coarse woody debris	Bog
	Fine woody debris	Both
	Standing dead	Both

Table 2.3. Mean alpha diversity measures for vascular species by plot (species richness- D_0, and number of species of equal abundance- D_1) and the Whittaker beta diversity (B_w) for the bog and fen based upon species presence/absence data collected in 2009. Different letter designations within a site denote significantly different means.

Site	Plot	Species D_0	Species D_1	Species B_w
Bog	Permafrost	$10.0^{a} \pm 0.8$	$5.79^{a} \pm 0.5$	0.36
	New Collapse	$4.83^{b} \pm 0.9$	$2.37^{b} \pm 0.4$	1.44
	Old Collapse	$4.50^{b} \pm 1.3$	$2.38^{b} \pm 0.4$	1.07
Fen	Control	$4.00^{a} \pm 0.0$	$3.47^{a} \pm 0.2$	0.25
	Lowered	$2.67^{b} \pm 0.3$	$2.28^{a} \pm 0.3$	0.88
	Raised	$4.67^{c} \pm 0.3$	$3.49^{a} \pm 0.5$	0.50

Table 2.4. Bog plant species Pearson correlations to non-metric dimensional scaling ordination Axis 1, and Axis 2 using plant species composition data.

Species	Axis 1	Axis 2
Eleocharis palustris	0.68	
Eriophorum vaginatum		-0.78
Feather moss	-0.66	
Ledum decumbens	-0.68	-0.90
Rubus chamaemorus		-0.78
Sphagnum	0.73	0.92
Vaccinium uliginosum	-0.75	
Vaccinium vitis-idaea	-0.73	-0.93

Table 2.5. Aboveground non-vascular NPP (g / m^2 / y) for moss functional groups in 2009 and 2010 at the bog and fen, scaled by abundance of each moss functional group. Values are means ± 1 SE where error estimates possible for each sampling technique and compounded across moss types for total error.

Year	Site	Plot	*Dicranum* sp	Feather	Brown	*Sphagnum* sp	Total
2009	Bog	Permafrost	2.0 ± 1.4	173 ± 60	0.0	76 ± 30	251 ± 220
2009	Bog	New collapse	0.0	0.0	0.0	324 ± 22	324 ± 22
2009	Bog	Old collapse	0.0	0.0	0.0	179 ± 11	179 ± 11
2010	Bog	Permafrost	1.3 ± 0.9	173 ± 60	0.0	119 ± 44	293 ± 252
2010	Bog	New collapse	0.0	0.0	0.0	377 ± 14	377 ± 14
2010	Bog	Old collapse	0.0	0.0	0.0	183 ± 9	183 ± 9
2009	Fen	Control	0.0	0.0	33 *	32 ± 15	65 ± 30
2009	Fen	Lowered	0.0	0.0	1.0 *	35 ± 15	36 ± 15
2009	Fen	Raised	0.0	0.0	15 *	40 ± 26	55 ± 36
2010	Fen	Control	0.0	0.0	27 *	17 ± 8	44 ± 21
2010	Fen	Lowered	0.0	0.0	0.4 *	15 ± 7	15 ± 7
2010	Fen	Raised	0.0	0.0	12 *	6 ± 4	18 ± 12

* Indicates estimated value using pure patch moss functional group NPP from Thormann et al., 1998

Table 2.6. Mean annual NPP (g / m^2 / yr) for vegetation types within each plot at the bog and fen as calculated for the summer of 2009. Values are means ± 1 SE for each sampling technique and compounded across sources of NPP for total error. Same letter designations indicate non-significant differences within a site for a given component of NPP.

Site	Plot	Tree	Understory	Moss	Belowground	Total
Bog	Permafrost	6.7 ± 0.5	91.8 ± 11[a]	251 ± 220	84.0 ± 14[a]	433 ± 391
Bog	New collapse	0	96.2 ± 8[a]	324 ± 22	13.0 ± 3[b]	433 ± 107
Bog	Old collapse	0	116 ± 18[a]	179 ± 11	72.4 ± 17[a]	368 ± 107
Fen	Control	0	303 ± 56[a]	65 ± 30	77.6 ± 23[a]	445 ± 260
Fen	Lowered	0	464 ± 245[a]	36 ± 15	69.5 ± 7[a]	569 ± 391
Fen	Raised	0	155 ± 68[a]	55 ± 36	61.9 ± 31[a]	272 ± 252

Table 2.7. Parameters from a vascular green area model for the bog and fen plots in 2009 and 2010. Data are means ±1 SE. DNC means model did not converge.

Site	Year	Parameter	Permafrost	New Collapse	Old Collapse
Bog	2009	VGA_{max}	D.N.C.	1.94 ±0.24	0.62 ±0.06
	2010	VGA_{max}	1.23 ±0.16	0.56 ±0.06	0.37 ±0.06
	2009	x_{max}	D.N.C	181.4 ±1.48	177.6 ±5.16
	2010	x_{max}	201.9 ±7.61	212.9 ±8.28	204.8 ±22.2
	2009	b	D.N.C	-12.31 ±1.66	28.9 ±7.49
	2010	b	41.2 ±17.1	40.63 ±11.6	65.7 ±58.7
Site	**Year**	**Parameter**	**Control**	**Lowered**	**Raised**
Fen	2009	VGA_{max}	3.07 ±0.48	3.36 ±0.38	3.32 ±0.63
	2010	VGA_{max}	1.96 ±0.25	4.55 ±0.55	2.42 ±0.50
	2009	x_{max}	178.1 ±12.3	186.1 ±5.05	170.4 ±54.7
	2010	x_{max}	201.6 ±8.5	203.2 ±4.08	215.8 ±15.9
	2009	b	35.86 ±19.1	32.34 ±9.6	55.59 ±84.5
	2010	b	48.72 ±17.7	-31.13 ±5.55	41.35 ±21.3

Table 2.8. Results of regression models analyzing the influence of 1) species abundance (% cover) on ANPP and biomass at the bog plots, and 2) species abundance on ANPP at the fen plots. Values marked with an asterisk are not significantly different from zero ($p > 0.05$).

Site	ANCOVA test	Plot	Coefficient	Parameter ± SE	95% CI (lower, upper)
Bog	Abundance vs. sqrt ANPP	Permafrost	Intercept	0.20 ± 0.25*	-0.29, 0.68
			Slope	0.19 ± 0.02	0.15, 0.23
		New	Intercept	0.68 ± 0.38*	-0.06, 1.42
			Slope	0.16 ± 0.04	0.08, 0.24
		Old	Intercept	0.69 ± 0.37*	-0.05, 1.42
			Slope	0.51 ± 0.10	0.32, 0.71
	Abundance vs. sqrt Biomass	Permafrost	Intercept	1.13 ± 0.67*	-0.20, 2.45
			Slope	0.30 ± 0.04	0.21, 0.39
		New	Intercept	0.83 ± 0.43*	-0.01, 1.68
			Slope	0.20 ± 0.02	0.16, 0.23
		Old	Intercept	1.90 ± 0.49	0.94, 2.86
			Slope	0.16 ± 0.02	0.12, 0.20
Fen	Abundance vs. sqrt ANPP	Control	Intercept	1.60 ± 1.2*	-0.77, 3.96
			Slope	0.47 ± 0.10	0.27, 0.67
		Lowered	Intercept	-0.14 ± 1.1*	-2.31, 2.02
			Slope	0.84 ± 0.11	0.63, 1.05
		Raised	Intercept	1.38 ± 1.34*	-0.20, 2.45
			Slope	0.32 ± 0.12	0.21, 0.39

Table 2.9. Fen plant species correlations to non-metric dimensional scaling ordination axes 1-3 based on plant species composition data.

Species	Axis 1	Axis 2	Axis 3
brown moss		-0.5	0.9
Carex atherodes	0.8		
Galium trifidum		-0.5	
Potentilla palustris	-0.5	-0.6	
Sphagnum sp.	-0.5	0.8	

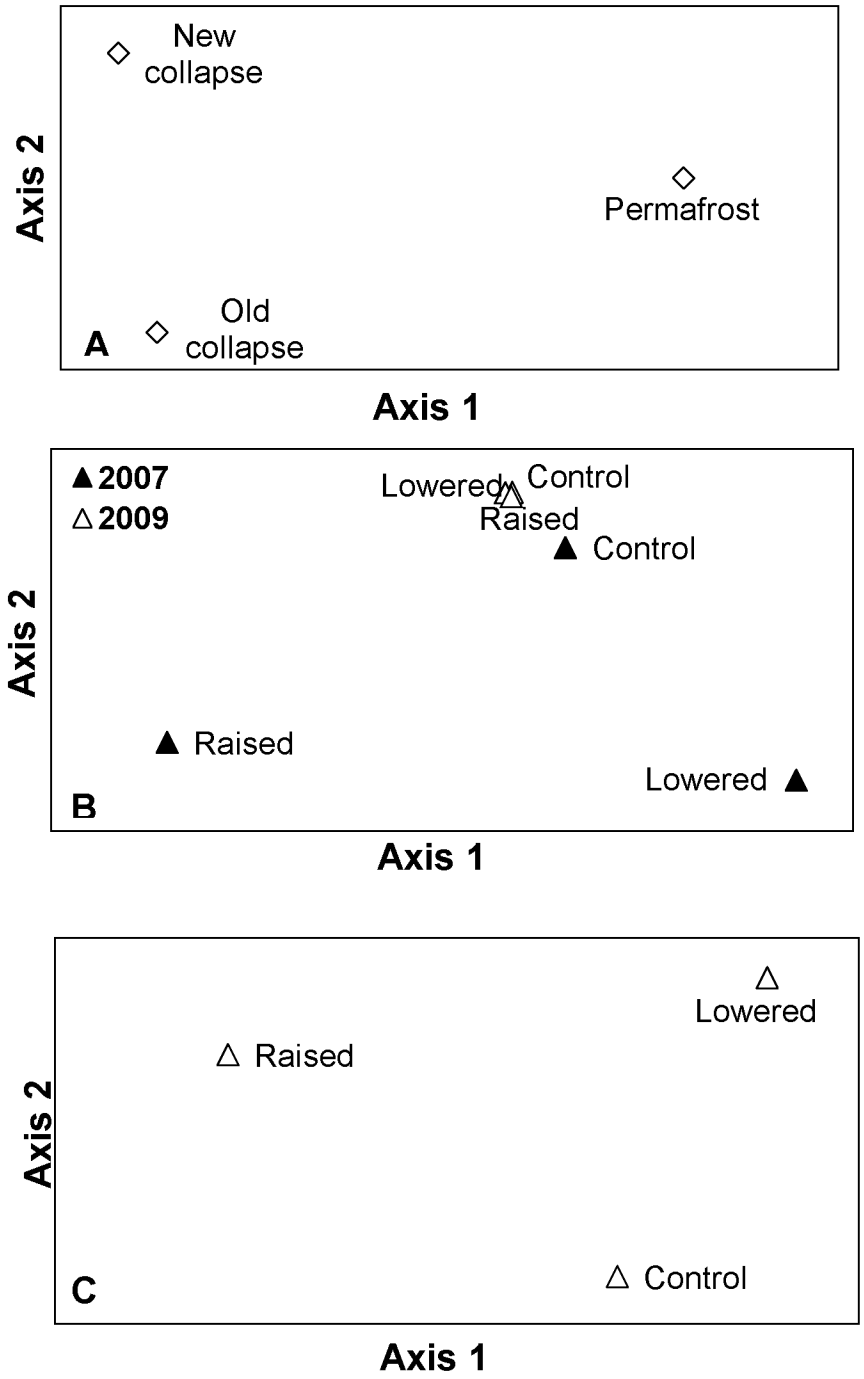

Figure 2.1. PCA ordination based on water table, and soil temperature data at 0 cm, 2 cm, 10 cm, and 25 cm below ground surface A) at the bog site in 2009, B) at the fen in 2007 (black) and 2009 (white) and C) at the fen site for 2009 only.

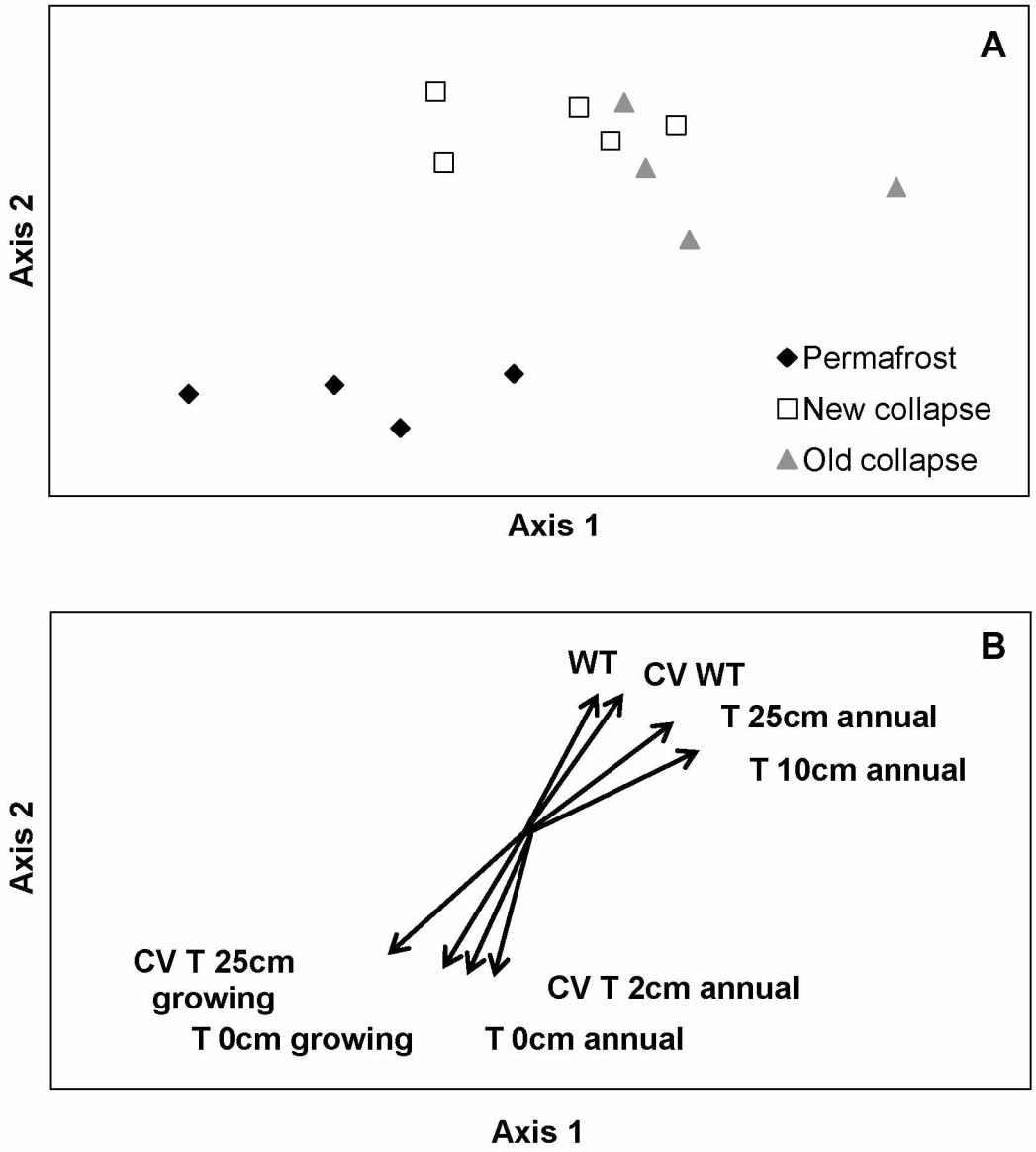

Figure 2.2. A) Results of a NMDS ordination of plant species abundance showing separation of the permafrost and collapse plots at the bog. B) The NMDS ordination including environmental variable correlations to species abundance as vectors.

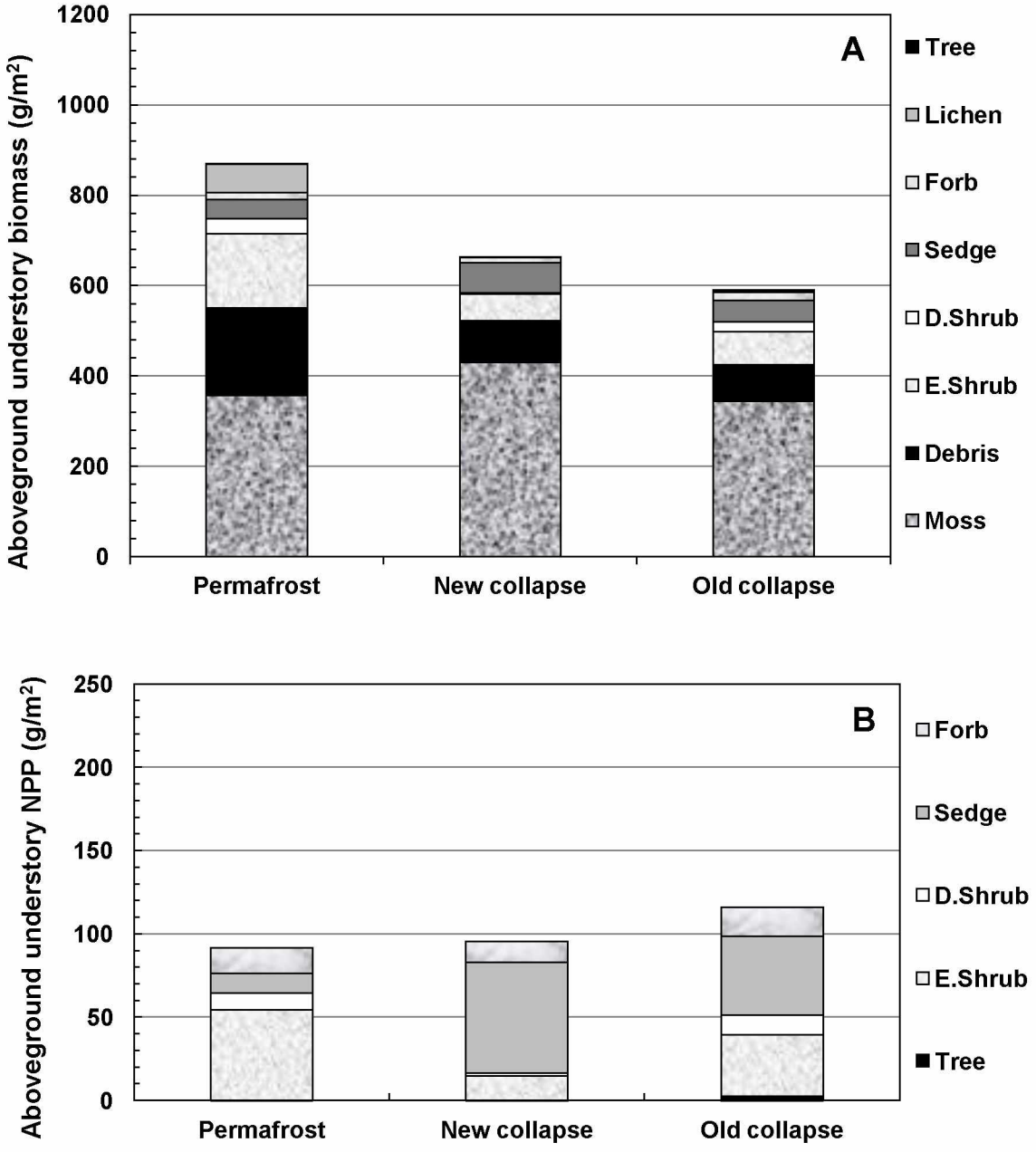

Figure 2.3. A) Mean aboveground peak biomass in 2009 (g / m^2) for understory species, including moss and litter, in the three bog plots. B) Net primary productivity (g / m^2 / yr) of aboveground vascular growth forms in the bog plots. Plant growth forms included forbs, sedges, deciduous shrubs (D. Shrubs), evergreen shrubs (E. Shrubs), all dead material as a debris category, moss, trees and lichen.

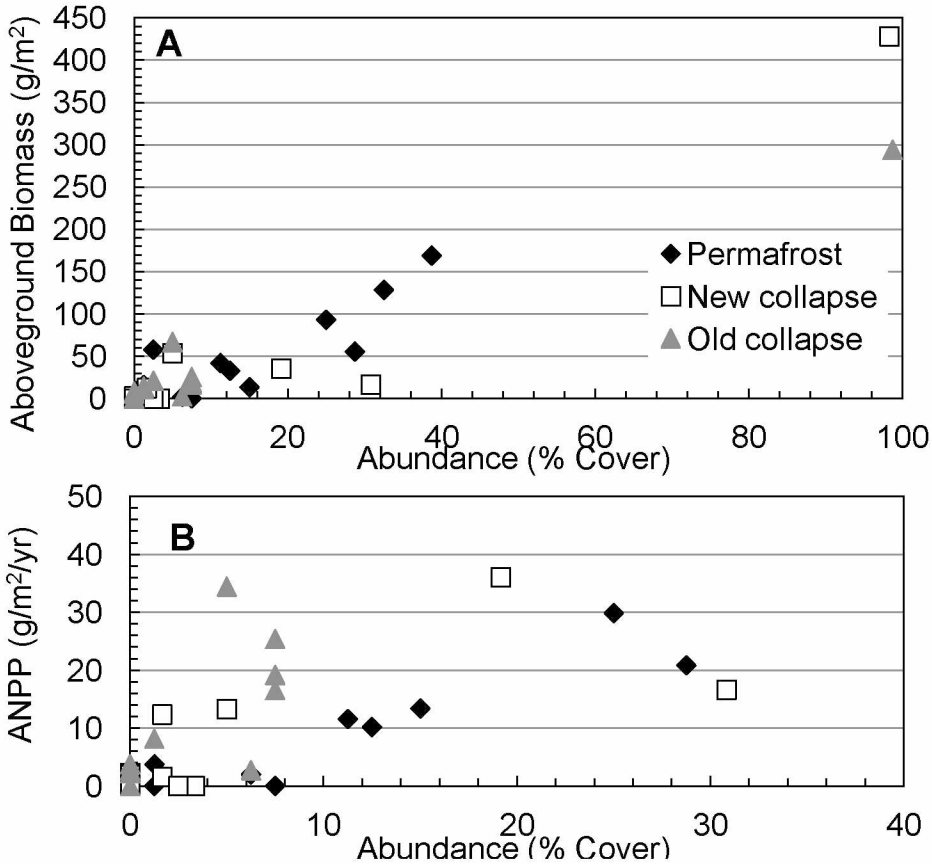

Figure 2.4. Structural relationships between A) aboveground biomass and abundance by plot mean for all species present within the three bog plots, B) aboveground productivity and abundance by plot mean for all species within each bog plot, as no differences in slope was detected between plots, the overall regression equation: Sqrt(ANPP) = 0.08 (Biomass) + 0.65 had an R^2 of 0.68 and the model p value < 0.001.

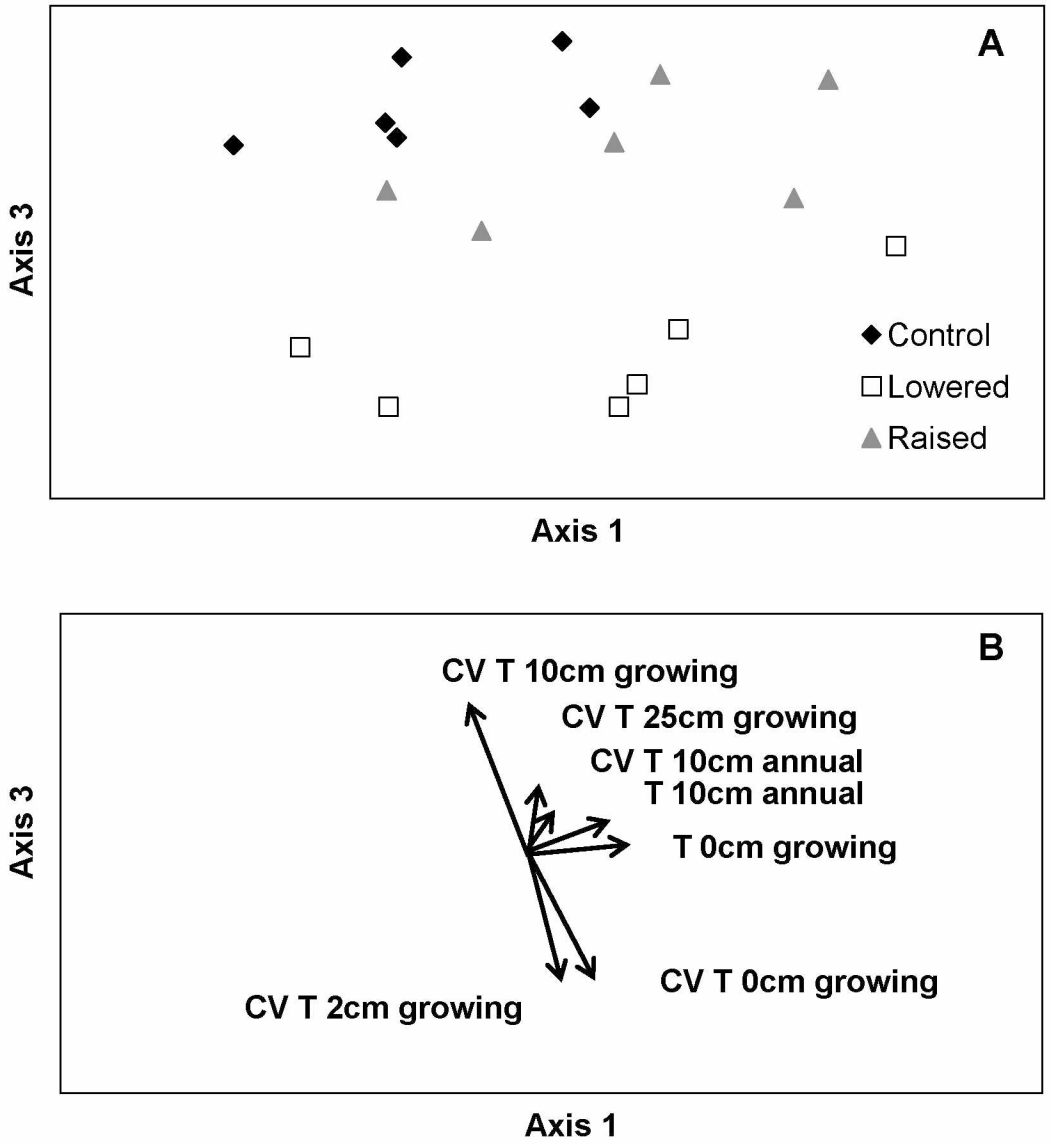

Figure 2.5. A) Results of a NMDS ordination of plant species abundance across the fen water table manipulation plots. B) The NMDS ordination portraying environmental variables correlated with species abundance as vectors.

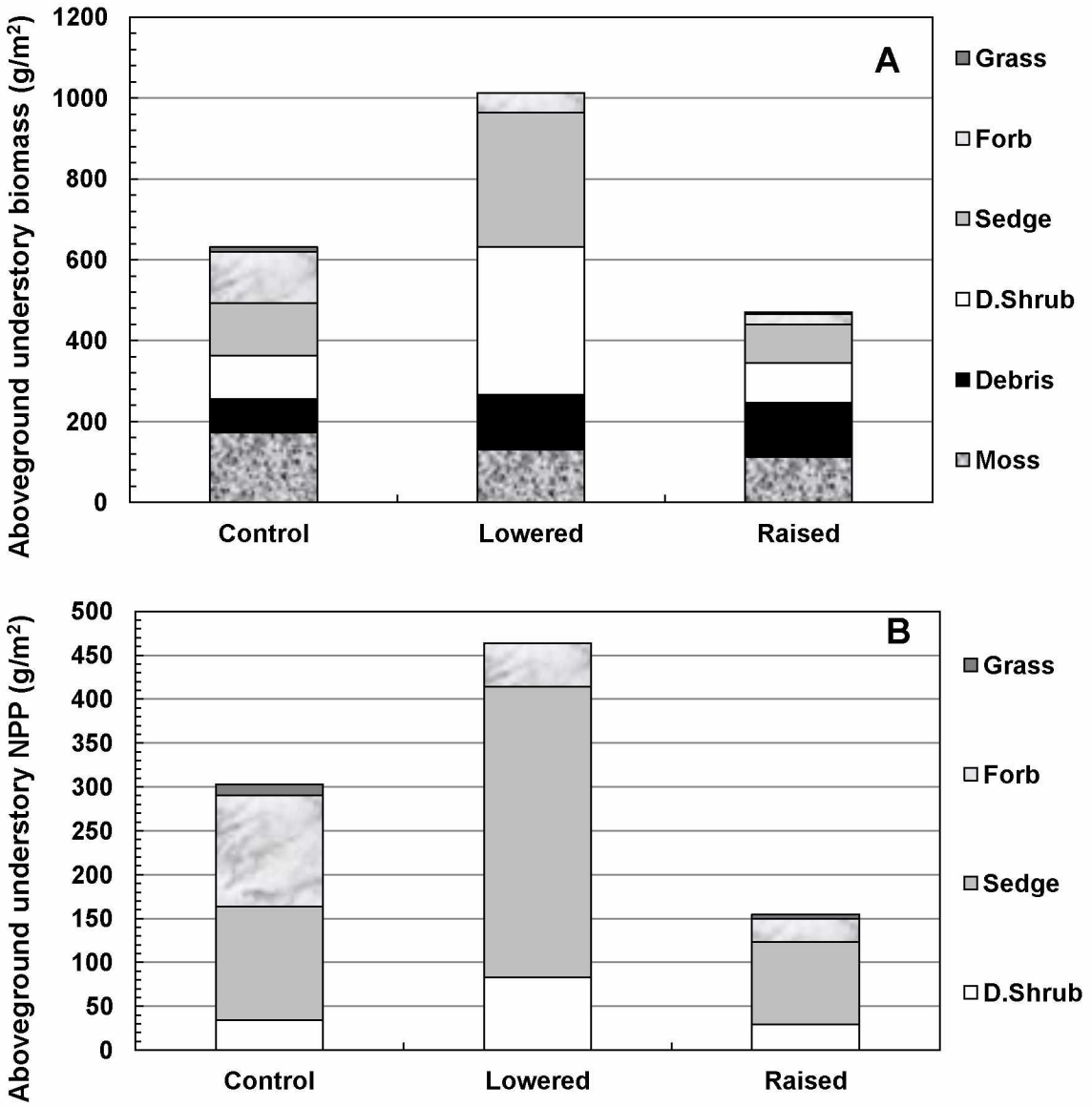

Figure 2.6. A) Mean understory biomass (g / m^2) of functional groups at the fen water table treatments B) Net primary productivity of the aboveground vascular layer by growth form at the fen water table treatments.

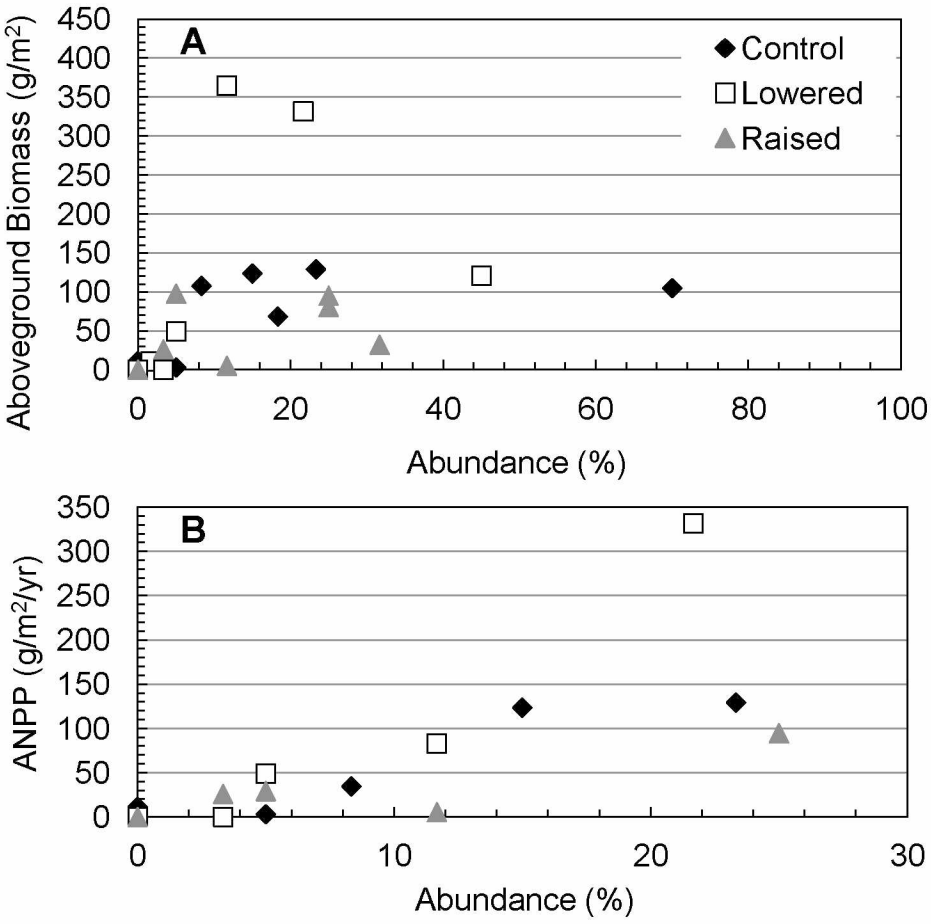

Figure 2.7. Relationships between A) aboveground biomass and abundance by plot mean for all species in a given plot within the fen. There were no plot differences in slope, site relationship sqrt(ANPP) = 0.20 (Abundance) + 1.53, $R^2 = 0.73$, *p* value <0.001, B) aboveground productivity and abundance produced different slopes between plots.

Chapter 3
Environmental and plant community physiological limitations on gross primary productivity in Alaskan boreal peatlands responding to climate change

I. Abstract

Net carbon sequestration in northern terrestrial regions has been heavily influenced by peatland ecosystems for the past 8,000 to 11,000 years. Peatlands, however, are currently facing increases in hydrologic disturbance associated with global climate change that may alter carbon accumulation associated with changes in the balance between gross primary production (GPP) and decomposition. This study examines the response in GPP to hydrologic disturbance in two peatland types, a bog and moderate rich fen, in boreal Alaska from 2007-2010. Rates of carbon uptake were greater at the fen than the bog for non-disturbed plots for all years except 2010, when the fen had lower uptake in response to low precipitation. At the bog, GPP of the newer collapse formation (~25 years old) was greater than at the non disturbed permafrost plateau and the older collapse formation (~45 years old) collapse. Although mosses were the most important contributor to GPP at the bog, differences in maximum vascular green area were responsible for differences in GPP among the plots. At the fen, the lowered water table treatment reduced GPP, but GPP of the raised water table treatment was not different from the non disturbed control. Although deciduous shrubs were the dominant plant growth form contributing to ecosystem GPP in the plots at the fen, the decreased moss cover at the lowered plot caused reduced GPP at this site. Furthermore, the negative relationship between maximum vascular green area and moss cover across the plots at the fen suggests a tradeoff between moss cover and vascular plant biomass that translates into reduced photosynthetic capacity under drying conditions.

II. Introduction

Despite a small global land area cover (approximately 7%), peatlands are important carbon sinks that have had a net cooling effect on global climate for the past 8,000 to 11,000 years (Frolking and Routlet, 2007; Yu et al., 2003). Nearly 90% of

peatlands are found in northern latitudes and boreal and subarctic peatlands cover 350 x 10^6 km^2 (24%) of the boreal forest (Moore et al., 1998; Vitt, 2006; Wieder et al., 2006). Peatlands generally form in areas where precipitation exceeds evapotranspiration rates, and where gross primary production (GPP) exceeds net losses of carbon from the system (Vitt, 2006). The total sequestration capacity of a peatland is therefore related to the balance between GPP and losses through mineralization/respiration of CO_2, leaching of dissolved organic carbon (DOC), methane efflux, and fire (Blodau, 2002; Chapin et al., 2006; Frolking et al., 2006).

Peatlands cover a substantial portion of the Alaskan landscape, with a total area of at least 8% (Bridgham et al., 2006). Based on carbon sequestration rates from Canadian peatlands, Alaskan peatlands store approximately 2.56 Tg C annually (Vitt et al., 2000). However there is significant variation in boreal peatland GPP on inter-annual and microtopographic spatial scales associated with variation in local environmental and biological controls (Alm et al., 1997; Bubier et al., 1999; Holden, 2005; Moore et al., 1998; Vitt and Chee, 1990).

Air temperatures have increased 1.3° C in the northern boreal zone over the past 50 years, and 3-7° C of additional warming is predicted to occur by the end of the 21st century (Chapin et al., 2010; Jorgenson et al., 2001). Predicted shifts in the timing and amounts of precipitation may lead to a deeper snow pack but provide only a small increase in annual precipitation that will likely not be significant enough to offset water losses associated with increased evapotranspiration (Chapin et al., 2010; Hinzman et al., 2006; Serreze et al., 2000). These climatic changes have the potential to influence a suite of environmental drivers within peatland systems that control C cycling, on a range of temporal and spatial scales, and may alter the frequency and severity of disturbance events (Blodau, 2002; Grosse et al., 2011).

Types of disturbance likely to influence the peatland systems of Alaska include drying associated with increased evapotranspiration and loss of permafrost (Riordan et al., 2006; Yoshikawa and Hinzman, 2003), and inundation associated with change in precipitation patterns and thermokarst collapse scar formation (Grosse et al., 2011;

Osterkamp and Romanovsky, 1999; Osterkamp et al., 2000). These disturbances can be considered hydrologic disturbances because they alter the availability of water in ways that will likely affect the balance between the uptake and loss of C from peatlands. Hydrologic disturbance in peatlands may affect plant-related processes such as photosynthesis and vegetation succession, and soil-related processes such as aerobic decomposition, production or oxidation of CH_4, and DOC leaching (Blodau, 2002; Grosse et al., 2011).

Studies have employed five general approaches to examine the influence of water availability and hydrologic disturbance on ecosystem processes in peatlands. These approaches involve analyses of: (1) inter-annual variability within the same site through time (Alm et al., 1999; Bubier, 2003; Lafleur et al., 2003); (2) spatial variability in processes of microforms within a site (Alm et al., 1997; Luken and Billings, 1985; Waddington and Roulet, 1996); (3) *in situ* manipulations of water table position in peatlands (Chivers et al., 2009; Chimner and Cooper, 2003a; Laine et al., 1995; Muhr et al., 2011); (4) observations of ecosystem functioning after natural disturbance (Camill et al., 2001); and (5) peat mesocosm or peat core studies where peat is removed from the site and environmental conditions are manipulated elsewhere (Aerts and Ludwig, 1997; Chimner and Cooper, 2003b; Updegraff et al., 2001).

Generally, results from natural and experimental drought in peatlands have found that a lowered water table increases aerobic respiration and nutrient mineralization but may result in reduced GPP associated with water stress (Alm et al., 1997; Lafleur et al., 1997; but see Chivers et al., 2009 and Muhr et al., 2011). Prolonged reduction of water availability may cause shifts in plant community composition from hydrophilic mosses towards more drought tolerant vascular species (Bubier et al., 1999; Laine et al., 1995; Murphy et al., 2009). In many cases this can lead to an increase in overall carbon uptake and storage in woody plant biomass (Laine et al., 1996). Manipulation studies have shown short-term increases in GPP in response to increased water availability associated with hydrologic disturbance (Chivers et al., 2009; Updegraff et al., 2001; but see Chimner and Cooper, 2003a). Comparisons across thermokarst gradients suggest that

GPP is higher in collapsed areas than in non-collapsed areas of the surrounding permafrost plateau (Myers-Smith et al., 2007; Wickland et al., 2006).

In this study I examine how natural and manipulated hydrologic disturbances affect GPP in Alaskan peatlands during the growing seasons of 2007-2010, which include substantial inter-annual variation in natural precipitation levels. I address three questions. First, how does GPP vary between a bog and a moderate rich fen, and how is GPP in each site influenced by hydrologic disturbance? In the bog, I quantified GPP in areas of intact and thawed permafrost. For the fen, I quantified GPP in a water table manipulation experiment with control, lowered water (drying) and raised water table (inundation) treatments. Second, how do environmental controls on GPP vary among these sites and types of disturbance? Third, how do plant community controls on GPP differ among these sites and types of hydrologic disturbance?

III. Methods

Field Site Description

Research was conducted at the Alaskan Peatland Experiment (APEX) located adjacent to the Bonanza Creek Experimental Forest (BCEF), within the Tanana River floodplain, approximately 35 km southwest of Fairbanks, AK (64.82° N, 147.87° W). The APEX project includes a moderate rich fen and a bog for examining the effects of artificially (fen) or naturally (bog) altered hydrology and soil temperature on C cycling processes in boreal Alaskan peatlands. The moderate rich fen site includes three water table manipulations that were established in 2005 and controlled by the pumping of groundwater; a control, a drained (lowered), and a flooded (raised) plot (Chivers et al., 2009; Chapter 2). At the bog site, plots represent differing ages of ground collapse associated with thermokarst formation from permafrost thaw. One plot was placed within the permafrost peatland plateau (permafrost plot), another in a recent thermokarst formation (collapse between 1983 and 1994 - new collapse plot), and a formation that began between 1972 and 1983 (old collapse plot); dates are based upon aerial

photography. For a detailed description of the vegetation and environmental differences between sites and plots within each site, see Chapter 2.

Gross Primary Productivity (GPP) flux

Data collection of ecosystem CO_2 flux was conducted using a clear static chamber and galvanized steel metal collars permanently placed in the peat surface (dimensions of 0.3721 m^2 by 26 cm deep). The gas flux chambers were constructed from a frame of 0.31 cm aluminum angle and covered with either clear 0.31 cm Lexan (bog) or FEP Teflon film (American Durafilm, Holliston, MA; fen). Both chamber types had a ground contact area of 0.3721 m^2 and a volume of 0.227 m^3 (226.981 L), and a removable Lexan top sealed using weather stripping to allow flushing of the chamber between flux measurements. A weather stripping seal was maintained between collar and chambers for all flux measurements.

At the bog site, collars were placed adjacent to existing boardwalk pathways to include representative microforms at the plot scale (lawns and hummocks). The new collapse plot contained 6 collars in 2008, 12 collars in 2009 and 9 collars in 2010, while the old collapse plot maintained 6 collars for all years included in this study. For the permafrost plot there were 3 collars in 2008 and 6 collars for both 2009 and 2010. Collar location for gas flux measurements at the fen site were placed in a grid pattern with 6 collars in each rectangular manipulation plot; 3 of these collars were used in a soil warming experiment (Chivers et al., 2009) and therefore not included in this paper. Flux measurements were conducted at each plot every 1-2 weeks from approximately mid-May through mid-September from 2007 in the fen or from 2008 in the bog through 2010. Measurements were only conducted on days without precipitation to avoid equipment damage; however measurements included overcast and smoky days.

Net ecosystem exchange (NEE) was measured based on changes in internal chamber concentrations of CO_2 over a two minute period, and measured in terms of carbon lost or gained to the atmosphere (negative values indicate carbon lost from the atmosphere to the ecosystem). Ecosystem respiration (ER) measurements were collected

as dark NEE fluxes, with a covering over the chamber to prevent photosynthesis. GPP was calculated as the difference between NEE and ER (Chapin et al., 2006). CO_2 concentrations ($\mu mol\ m^{-2}\ s^{-1}$) and % relative humidity were measured using an EGM-4 infra-red gas analyzer by PP Systems (Amesbury, MA) with an internal pump, and data were collected every 1.6 seconds during each sample period. PAR ($\mu mol\ m^{-2}\ s^{-1}$) and air temperature (°C) within the chamber were measured simultaneously using a TRP-1 Temperature/PAR probe by PP Systems. Two fans within each chamber facilitated air circulation and temperature evenness. Flux measurements were checked for quality control in cases where the correlation coefficient between CO_2 concentration and time was less than 0.8; however flux measurements were only excluded if the data indicated an equipment malfunction or highly improbable values were detected (less than 0.8 % of data were removed).

GPP measurements were analyzed using repeated measures analysis of variance in Proc Mixed (SAS v. 3.1) and Tukey's post hoc comparison of means (Chivers et al., 2009) to determine how carbon uptake by the ecosystem was influenced by hydrologic disturbance (plots within a site), differences among years, and any interaction between plots and years. Because the plots at the bog and the fen were not replicated, the collars within each plot are used in the statistical analysis as pseudo-replicates for the plot treatment. Thus, my inferences are limited to the specific plots I chose for this study.

Environmental variable measurements

LIGHT

CO_2 exchange measurements were collected under a range of ambient and manipulated PAR intensities. I used fabric shrouds to block approximately 50% or 25% of incoming light for manipulated PAR intensities, and the measurements of CO_2 exchange associated with manipulated PAR intensities were collected at each collar within a few minutes of the CO_2 exchange for ambient PAR conditions. GPP values from both the shrouded and unshrouded measurements were used to develop relationships

among photosynthesis, PAR intensities, and water table position at the plot scale; these shrouded measurements were not used for the plot scale comparisons described above.

WATER AVAILABILITY

The water table position was assessed using bubble tubes in wells established within the peat column measured concurrently with gas flux measurements. Wells were located immediately adjacent to gas flux collars at the fen site (n=3 per plot), and included two wells per plot for the old and new collapse plots at the bog site. The permafrost plot at the bog site had no existing water table most of the year, due to a shallow thaw depth. This effectively made the thaw depth and water table depth equivalent in limiting below-ground processes associated with water and nutrient availability, and controlling factors such as rooting depth. Although there are key differences between a water table depth and thaw depth, especially relating to changes in temperature with depth, I used thaw depth at the permafrost plot as a proxy for water table in developing models of GPP dependency on environmental controls. Depth to frost, or seasonal thaw depth, was measured using a metal rod of known length inserted into the peat column until frozen ground was reached. These measurements were collected adjacent to each gas flux collar concurrently with carbon flux measurements.

Soil moisture of the top 10 cm of peat was estimated using volumetric water content determined by a ML2x ThetaProbe Soil Moisture Sensor (Dynamax, Houston, TX). Measurements were collected every week during the growing season from 2007 to approximately mid July 2010 in coordination with carbon flux measurements at each gas flux collar. For 2008, 2009 and 2010 two estimates of soil moisture per collar were recorded for accessible hummocks and hollow/lawns. Recordings measured on days when the water table was above the surface of the peat were assigned a value of 100% soil moisture. Plot scale recordings of continuous soil moisture were monitored starting in August 2009, using CS615 or CS616 soil moisture sensors installed at 5, 10 and 25 cm depth and collected with CR10X dataloggers (Campbell Scientific Inc., Logan, UT).

DATA ANALYSIS OF GPP AND ENVIRONMENTAL VARIABLES

Examination of environmental variables influencing GPP were determined using Proc NLIN in SAS following the model applied in Chivers et al. (2009) (Equation 1). Non-linear parameters were also calculated for each collar within a plot, and these estimates were statistically compared among plots. The mean of collar parameter calculations was then compared with the plot scale parameter estimates as a measure of model convergence and robustness (Shaver et al., 2007). All models were compared using the percent of variation in measured GPP explained by the given model. For Equation 1, PPFD (photon flux density; PAR measurements above) and WT (water table position) were measured variables. Estimated parameters include $P_{MAX(PPFD,WT)}$, which is the rate of maximum photosynthesis under light saturated conditions when the water table was at an optimum position for photosynthesis; k, which is the photon flux density at which GPP was equal to half P_{MAX}; uP, which is the optimal water table position for photosynthesis; and tP, which is a measure of variance in the amplitude of water table position (Tuitilla et al., 2004).

Equation 1 ——— ———

Physiological variable measurements

EVAPOTRANSPIRATION (ET)

Evapotranspiration measurements using static flux chambers allowed a direct comparison of water loss limitations and carbon uptake for plant communities under differing levels of soil water availability. Air temperature (°C) and relative humidity were measured continuously during GPP measurements, allowing for calculation of localized rates of ET (McLeod, 2004) and tradeoff comparisons between water loss and carbon uptake.

Air temperature and relative humidity were used to calculate the rate of vapor density increase, following the methodology given by McJannet et al. (1996). The calculations associated with vapor pressure components, and the final calculation of evapotranspiration (mm / h), are outlined in detail in McLeod et al. (2004). For

determining the linear portion of the relationship between vapor density and time, data were collected between 0 and 48 seconds, and deviances were checked for correlation coefficients below 0.8. Deviance from calculation of the linear portion of the flux was corrected by altering the length of the collection period as necessary to include the linear portion of each flux (increased or decreased). Measured instantaneous evapotranspiration was regressed against GPP using a general linear model for each plot at both the bog and fen sites, and the slope coefficients and their standard errors were compared among plots within a site.

VASCULAR GREEN AREA (VGA)

The vascular green area (VGA) for each vascular species was measured (leaf area m^2 / ground area m^2) for all plots at both the bog and fen sites over the growing seasons of 2009 and 2010 as reported in Chapter 2. Leaf area measurements of dominant species were conducted every two weeks, to calculate the surface area (m^2) as it changed over the summer season. The change in VGA through time was modeled using non linear regression (Wilson et al., 2007; SAS 9.1, SAS Institute) in which total VGA for a given flux collar was the summed total for individual species, as reported in Chapter 2.

PLANT COMMUNITY COVER

All vascular species were identified and assigned to functional groups as in Chapter 2. Plant growth form groups included grasses, sedges, herbaceous forbs, evergreen shrubs, deciduous shrubs, seedling trees, lichens, *Sphagnum*, *Dicranum*, feather moss and brown moss. Species nomenclature followed Hultén (1968) with the exception of sedges (Tande and Lipkin, 2003). Lichens, when present, and mosses where keyed to genera rather than species, with mosses following Seppelt et al. (2008).

Visual estimation of the vegetation community cover by percent for ground layer species was determined independently for each species present within the gas flux collar. Moss functional groups were estimated out of a total ground area of 100%. Visual estimates were conducted every 2-4 weeks from 2008-2010 by the same individual to

avoid error associated with different observers. Cover was estimated to whole percent integers, except for species with only 1-2 stems present in the collar, which were treated as trace species with 0.1% cover.

LINKING STRUCTURE AND FUNCTION: GPP AND COMMUNITY CONTRIBUTIONS

The relative contribution of each plant growth form group to ecosystem GPP flux measurements were considered by estimating growth form group specific parameters based on VGA (m^2 / m^2) measurements for vascular growth form groups, and percent cover of moss groups. To accomplish this, P_{max} was partitioned into rate-limiting photosynthesis parameters per VGA (for vascular plants) or percent cover (mosses) using estimated parameters, estimated using non-linear modeling, for each plant growth form group ($V_{group1} \rightarrow V_{groupn}$) multiplied by the VGA or percent cover of the plant growth form group. Vegetation parameters were estimated following Equation 2 using plot scale environmental parameters (k, uP and tP) calculated in Proc NLIN (SAS 9.1).

Equation 2 ——— ———

PPFD, WT, k, uP, and tP are as defined in Equation 1, *i* is a subscript for designating individual measurements, *j* is a subscript for plant growth form types within a plot, *n* is the total number of plant growth form types within a plot, V_{groupj} is the rate-limiting photosynthesis parameter for plant growth form group *j*, and VGA_{ij} is the vascular green area or percent cover (for mosses) of growth form group *j* for GPP measurement *i*.

I analyzed correlations between GPP and VGA_{max} among plots within a site during 2009 and 2010 to directly determine whether growing season averages of GPP were associated with maximum vascular photosynthetic area. Additionally, maximum photosynthesis rates (P_{max}) for each plot at the bog and fen were regressed against VGA_{max} to examine whether differences among plots at a site were related to vascular photosynthetic area. For examining the relationship between non-vascular and vascular

cover at both sites I also compared VGA_{max} and percent cover of moss using linear regression to determine potential tradeoffs.

IV. Results

Environmental variables

BOG

Water table position at the new collapse remained similar throughout the growing season for 2008 and 2009, staying above the peat surface. However, in 2010 the water table dropped below the surface shortly following snow melt and remained constant throughout most of the summer, responding to August precipitation events for a brief time rising above the surface. The old collapse plot showed overall the same trends for 2008 and 2009, with a gradual lowering of the water table over the growing season to below the peat surface, and then an increase in August in response to rain events that did not result in water above the surface. During 2010 the water table position began below the peat surface, and steadily continued to drop throughout the growing season. Soil moisture measurements showed high variation among days, although in general the new and old collapses followed the same patterns of drying and re-wetting. The rate of thaw to talik, or ground that does not freeze in winter despite adjacent permafrost, in both the new and old collapse was similar between years. The permafrost plot remained consistently drier than the collapse scar formations across all years. The thaw depth progression over the course of the season showed linear trends over time for all years (2008-2010) (all plots $R^2 > 0.80$). The permafrost plot consistently thawed to a depth of approximately -45 cm by Sept 7th (Julian date 250) in each year, and the rate of thaw over time was similar among years. Thaw depth at the permafrost plot was used as a proxy for water table position.

FEN

At the fen in 2007, a climatically typical year, the water table in the lowered and raised plots tracked the control plot as designed (approximately 10 cm difference). In

2008, all the manipulation plots experienced high water tables at the start of growing season related to snow melt runoff from the surrounding uplands that was not observed in other years reported in this study. Precipitation in the second half of the 2008 growing season caused the water table to rise above the peat surface across all manipulation plots (Kane et al., 2010). The high water table at the end of the 2008 growing season froze, and then thawed out in the spring of 2009 leaving high water table positions across all plots, and prevented the manipulation from being maintained in that year. All the plots experienced a gradual drop in water table over the course of the growing season, ending more than 5 cm below the peat surface. The water table in the summer of 2010 began below the peat surface and continued to drop across all plots throughout the season, ending below many of the wells by early August, although the manipulation was maintained between water table treatments. Seasonal trends in soil moisture measurements were limited by substantial inter-annual differences in water table position, but in general showed drier soils when the water table was lower across the plots at the site. The thaw depth throughout the season increased linearly with time at a similar rate across all plots in 2007 and 2010 ($R^2 > 0.80$). The thaw depth in 2008 increased with linearly with time, but later in the growing season it increased exponentially with time because of the high thermal conductivity for the fully saturated soil column. The thaw depth in 2009 followed this exponential pattern, reaching talik because of the high water table.

Gross Primary Productivity (GPP)

BOG

At the bog site, mean growing season GPP was significantly different among the permafrost, new collapse and old collapse plots (**Table 3.1; Figure 3.1A**). Multiple comparisons analysis determined that the new collapse was different from both the permafrost plot ($df = 25$, $t = -3.11$, $p = 0.0.0123$) and the old collapse ($df = 25$, $t = -3.67$, $p = 0.0032$), while the permafrost plot and old collapse were not different ($df = 25$, $t = -0.46$, $p = 0.8914$). Although GPP was not significantly different among years, there was a

significant interaction between plot and year. Multiple comparison analysis of this interaction term indicates that the new collapse had greater carbon uptake in 2008 than 2010 (df = 32, t = -4.31, p = 0.0040), while the permafrost plot had less carbon uptake in 2008 than both 2009 (df = 32, t = 4.18, p= 0.0058) and 2010 (df = 32, t = 7.23, $p <$ 0.0001). The old collapse plot did not vary significantly in GPP among years of data collection.

FEN

At the fen site, GPP was significantly different among years and among plots (**Table 3.1**; **Figure 3.1B**). In general, 2009 (the post-flood summer) was the year with the greatest carbon uptake across all plots, while 2010 (a drought summer) had the lowest carbon uptake. Multiple comparisons analysis among years with significant differences are shown in **Table 3.2**. Multiple comparisons analysis among plots indicated that the lowered water table plot was consistently taking up less carbon than the control plot (df = 6, t = -6.29, p = 0.0.0018) and the raised plot (df = 6, t = 5.97, p = 0.0024). The control and raised plots were not statistically different from each other (df = 6, t = -0.14, p = 0.9888). The interaction between year and plot was significant (df = 18, F = 3.38, p = 0.0207), and was primarily driven by substantial increases in GPP for the control plot in 2009 (**Figure 3.1B**).

Relationships between GPP and environmental variables

BOG

The PAR intensities ranged from 27.13 to 1946 (μmol m^{-2} s^{-1}), with a mean of 708.9 (μmol m^{-2} s^{-1}; standard deviation: 410.1, n = 1434). There was close agreement between plot-based estimates (**Table 3.3**) and the mean of the collar-based estimates of parameters in Equation 1 (not shown), except for the permafrost plot in which the non-linear model did not converge on parameter estimates for any of the collars. This lack of convergence may be related to the fact that thaw depth was used as a proxy for water table depth at the permafrost plot. Eleven collars in the new collapse plot and 5 collars in

the old collapse plot converged. Comparison of collar-based estimates between the new and old plots revealed a significant difference in the log-transformed (for normality assumptions) P_{max} estimates (df = 14, F = 8.21, $p = 0.0125$). The log-transformed half saturation light parameter (k) was not significantly different between the new and old plots (df = 14, F < 0.0001, $p = 0.99$). Similarly, the water table related parameter uP estimate was not significantly different between the plots (df = 14, F = 3.22, $p = 0.0942$), but tP estimates were significantly different between the plots (df = 14, F = 10.74, $p = 0.0055$).

FEN

At the fen, PAR light intensities ranged from 26.3- 2224 (μmol m^{-2} s^{-1}), with an average of 702 (μmol m^{-2} s^{-1}; standard deviation: 478.2, n = 726). There was close agreement between plot-based-estimates (**Table 3.3**) and the mean of the collar-based estimates of parameters in Equation 1 (not shown). All collars in all plots converged in estimates parameters for Equation 1. P_{max} (log transformed), k, uP, and (log transformed) tP were not significantly different among plots (P_{max}: df = 6, F = 3.02, $p = 0.124$; k: df = 6, F = 1.36, p = 0.325; uP: df = 6, F < 0.0001, $p = 1$; tP: df = 6, F = 0.15, $p = 0.865$).

Relationship between GPP and physiological variables

EVAPOTRANSPIRATION (ET)

Bog

Analysis of the linear relationship between measured GPP and ET for each plot at the bog indicates a weakly significant coupling between carbon uptake and water loss through evapotranspiration at the collapse plots, but not at the permafrost plot (**Table 3.4**). GPP and ET were more tightly coupled at the old collapse plot than at the new collapse plot, and the greater slope at the old collapse plot indicates it had higher water loss relative to carbon uptake.

Fen

At the fen, GPP and ET were weakly coupled at all of the plots (**Table 3.4**), and the coupling was weakest at the control plot. The lowered water table plot had the greatest water loss per carbon uptake, and the control plot had the least water loss relative to carbon uptake.

LINKING STRUCTURE AND FUNCTION: GPP AND COMMUNITY CONTRIBUTIONS

Bog

At all of the plots of the bog site, the partitioning of P_{max} revealed that *Sphagnum* mosses contributed the greatest proportion of ecosystem GPP for all plots, with the highest contribution at the new collapse plot (**Table 3.5**). GPP at the permafrost plot also had strong contributions from feather and *Dicranum* mosses, in addition to forbs and deciduous shrubs. At the new collapse, GPP also had contribution from sedges, while GPP at the old collapse had similar contributions from forbs and sedges. Univariate plots between GPP for standardized environmental conditions and either VGA or percent cover for the different plant growth form groups supported the above evaluation of the relative contribution to GPP per plant growth form group (see **Appendix**).

There was substantial variability in VGA_{max} among the plots at the bog (**Figure 3.2A**) that is unrelated to moss cover (**Figure 3.3**). Although mosses had the greatest contribution to GPP within each plot of the bog site, variability in the VGA_{max} across plots and years explains variability in plot-scale GPP ($R^2 = 0.73$, **Figure 3.4A**) as plot-scale P_{max} appears to increase with mean VGA_{max} across years (**Figure 3.4B**).

Fen

In contrast to the bog, vascular plants contributed more to GPP at the fen than mosses (**Table 3.5**). Deciduous shrubs contributed the most GPP at each plot, with the strongest contribution at the control plot. Secondary contributions to GPP from other plant growth form groups came from forbs and *Sphagnum* at the control plot; from grasses, forbs, and sedges at the lowered plot; and from forbs, grasses and brown moss at

the raised plot. Univariate plots between GPP for standardized environmental conditions and either VGA or percent cover for the different plant growth form groups supported the above evaluation of the relative contribution to GPP per plant growth form group (see **Appendix**).

There was substantial variability in VGA_{max} among the plots at the fen (**Figure 3.2A**) that is related to lower moss cover at the lowered water table plot (**Figure 3.3**). In contrast to the bog, plot-scale GPP of the fen is not related to VGA_{max} ($R^2 = 0.0004$; **Figure 3.4A**).

V. Discussion

The influences of hydrologic disturbance on GPP

Previous work on comparing rates of carbon uptake for different peatland types have shown an increase in GPP associated with nutrient status, from bogs < poor fen < moderate rich fen < rich fen < extreme rich fen, under non disturbed conditions (Bubier et al., 1998). Comparison of GPP between plots without hydrologic disturbance, the permafrost plot at the bog and the control plot at the fen site, also suggests that the fen takes up more carbon than the bog. Hydrologic disturbance at the bog resulted in the greatest GPP at the new collapse and at the fen it resulted in the reduced GPP at the lowered plot. However, it is likely that the permafrost plot has higher rates of carbon uptake than the old collapse plot because the GPP estimate of the permafrost plot does not include tree GPP.

Previous research on GPP and productivity in permafrost peatland complexes has focused on differences between permafrost plateaus and collapse scar formations, and has assumed that collapse scars within a bog complex are comparable (Camill, 1999; Turetsky et al., 2007; Wickland et al., 2006). Results from this study suggest that age of collapse should be considered as a variable in understanding variability in GPP across the landscape.

I found that hydrologic disturbance at the fen resulted in the reduced GPP at the lowered water table plot. Water table manipulation studies have produced contradictory

results on productivity responses, especially related to differences in temporal and spatial scale (Chimner and Cooper, 2003a; Chivers et al., 2009; Laine et al., 1995; Muhr et al., 2011; Updegraff et al., 2001). Short term studies, which focus on initial or immediate responses of peatlands to changes in water availability, have frequently shown reduced productivity in both the vascular and non-vascular functional groups present in response to drying and increased CO_2 uptake with increased water availability (Alm et al., 1999; Updegraff et al., 2001). Studies that have examined species composition changes associated with prolonged hydrologic disturbance instead report increased storage of C in woody tissues of shrub and tree layers and greater CO_2 uptake for plant communities that have higher abundances of shrubs (Bubier, 2003; Laine et al., 1995). My study, which examined the impacts of hydrologic disturbance on GPP during years 3-6 post manipulation in the moderate rich fen, found a similar response of reduced GPP in the lowered plot that was documented by Chivers et al., (2009) for years 1-2 post manipulation.

Many peatland studies have documented the effects of inter-annual variation in environmental controls, especially water table and temperature, on changes in annual carbon uptake (Alm et al.,1999; Bubier, 2003; Thormann et al., 1998). This study documents 3-4 years of variation in GPP responses to both flooding and drought in Alaska boreal peatlands. For the summer of 2008 the APEX sites received 131.63 mm of rain between May 15th and September 15th, while the sites received 96.8 mm and 103.76 mm of rain during this time period in 2009 and 2010, respectively. During July of 2009 only 1.25 mm of rain fell, and so while residual flood waters from 2008 offset the immediate effect of this drought in the fen, there was no recharge of the ground water from surrounding uplands.

Drier conditions for the bog permafrost plot favored the drought tolerant shrub and seedling trees and increased rates of GPP between 2008 and 2010. Within the collapse scars however, little rain input for 2009 and 2010 resulted in lower GPP in 2010 for the new collapse. The lack of an annual effect in GPP rates at the old collapse plot is likely related to an increased peat deformation and mobility associated with the water

table position, where the peat column compressed and expanded with available water in the old collapse more so than in the new collapse (Lawrence, 2010). At the fen there were differences between the control plot and the manipulation plots. Statistically the lowered and raised plots were unresponsive to inter-annual variation in environmental conditions, while the control plot had the greatest GPP under the transition from flooded to unflooded conditions in 2009 and the lowest GPP in 2010 during drought conditions.

Influence of environmental controls on GPP

The influence of environmental controls on peatland GPP has been studied in a range of peatland types (Bubier et al., 1998; Muhr et al., 2011; Riutta et al., 2007; Updegraff et al., 2001); however there are few studies that include thermokarst bogs and rich fens located within the discontinuous permafrost zone of the boreal forest (but see Chivers et al., 2009; Myers-Smith et al., 2007; Wickland et al., 2006). Specifically, the influence of environmental variables identified as main controls on GPP in peatlands have not been well quantified within collapse scar formations or within the surrounding peatland plateau. At the bog, P_{max}, the parameter for carbon uptake under optimum conditions, was greatest in the new collapse and least in the old collapse. This is similar to the pattern of NPP among plots documented in Chapter 2. The half saturation constant for light-limited photosynthesis was substantially less at the permafrost plot than at the collapse plots, and is likely related to the influence of light competition from the black spruce overstory in addition to a species composition with greater shade tolerance in areas without disturbance (Laine et al., 1995). The parameters associated with water table position, uP and tP, were also different between the permafrost and the collapse plots, based on plot scale parameter estimation, which suggests that water table has very different controls over GPP in these types of plots.

Measurements of the effects of environmental controls on the water table manipulation plots at the fen were reported for the first two years of manipulation by Chivers et al. (2009). That study focused on short-term responses to water table draw down, and consequently reported high error associated with environmental parameter

estimates that control GPP (Chivers et al., 2009). Results from this study examine similar contributions of environmental conditions to GPP. However, parameter estimates are based on the succeeding 4 years of data, which include much more substantial variation in climatic conditions. The P_{max} parameter estimates in this study confirmed a pattern of raised > control> lowered manipulation plots documented by Chivers et al. (2009), although the differences among the plots were not significant in this study. In comparison to Chivers et al. (2009), this study estimated lower k values on all fen plots, but the k values I estimated in this study were within the range of uncertainty from Chivers et al. (2009). Both of the parameters related to water table, uP and tP, were estimated to be much larger in this study than by Chivers et al. (2009), which I interpret as being related to both higher water tables in 2008 and 2009 as well as more water table variability among the years of this study (2007-2010) in comparison with 2005 and 2006.

Plant community controls on GPP

Examination of the influence of the plant community composition on GPP has been addressed in previous studies using a variety of techniques. Many studies target single species plots and compare rates of carbon uptake assuming similar environmental conditions between spatially distinct areas (Alm et al., 1999; Bubier et al., 1998; Riutta et al., 2007; Shaver et al., 2007). Other methods have used physiological relationships to examine relationships between peatland structure and productivity (Chivers et al., 2009; Tuittila et al., 2004). The low correlation between ET and GPP indicates that ecosystem carbon uptake is largely uncoupled from water loss, but this relationship doesn't shed any light on whether mosses or the vascular component of the plots are more important in terms of carbon uptake. Also, hydrologic disturbance plots at both the bog and fen in this study have different species composition, thereby preventing patch comparisons for species contributions to ecosystem carbon uptake. Instead, I used a number of physiological comparisons and attempted to partition P_{max} within each plot into parameters that reflect the relative contributions from vascular and non-vascular plant growth forms (Equation 2). I also examined relationships between VGA_{max} and moss

cover, GPP and VGA_{max} and P_{max} and VGA_{max} to understand the role of different plant growth forms in carbon uptake among plots at a site.

At the bog, mosses were the most important contributor to GPP, which is consistent with the NPP results reported in Chapter 2. This suggests that the partitioning of P_{max} may provide a means of ascribing contributions to GPP. Although mosses were the most important contributor to GPP, differences in VGA_{max} among the plots were responsible for differences in GPP among the plots. The positive relationship between P_{max} and VGA_{max} among plots supports this interpretation.

At the fen, deciduous shrubs were the dominant plant growth form contributing to ecosystem GPP, which was also consistent with the NPP results reported in Chapter 2. In contrast to the bog, plot-scale GPP of the fen was not positively related to VGA_{max} primarily because the lowered plot had the greatest VGA_{max} and the least GPP. The lowered plot decreased in moss cover in comparison to the control, a result consistent with many long-term drawdown experiments (Alm et al., 1999; Laine et al., 1995; Murphy et al., 2009). The fact that plot-scale P_{max} was smallest at the lowered plot where VGA_{max} was greatest suggests that the loss of moss photosynthetic capacity was responsible for the general loss of photosynthetic capacity at this plot. Furthermore, the negative relationship between VGA_{max} and moss cover at the fen suggests a tradeoff between moss cover and vascular plant biomass under drying conditions. Specifically, the increase in VGA_{max} at the lowered plot was related to an increase in leaf area of the deciduous shrub species (*Potentilla palustris*).

VI. Conclusion

Generally GPP was higher at the control plot of the fen than the permafrost plot of the bog, however during the driest summer (2010) this pattern was reversed. Among water table manipulation plots at the fen, the lowering of the water table reduced GPP in comparison to the control, while the raising of the water table increased GPP. The control plot exhibited inter-annual variability in response to annual climate conditions, and took up more carbon under the more saturated conditions of 2009, declining in carbon uptake

in the summer of 2010. Results from the bog suggest that not only were there also differences between the permafrost plateau and the thermokarst formations, there were differences in carbon uptake between thermokarst formations of differing ages since collapse. Further, the old collapse plot had reduced carbon uptake relative to the permafrost plateau, suggesting a need for greater understanding of the spatial and temporal variation in carbon uptake within collapse scar formations.

There were no distinct patterns in peatland type response to environmental conditions; P_{max} at the permafrost plot of the bog was less than the P_{max} of the fen control plot however it was higher than the lowered water table plot P_{max}. Additionally, the new collapse P_{max} at the bog was comparable to the control and raised plots at the fen. There was high variation in water table position for all plots, especially in the lowered plot at the fen, associated with the climatic extremes during the course of this study.

Partitions of P_{max} by plant growth form showed that *Sphagnum* contributed the most to ecosystem GPP at all bog plots, while deciduous shrubs contributed the most to GPP for all plots at the fen. These results are consistent with NPP measurements reported previously from the same plots. Differences in GPP among plots however, were attributed to changes in VGA at the bog, where increased vascular cover also increased P_{max} and GPP. At the fen a reduced cover of mosses at the lowered plot produced a reduced level of carbon uptake, with a tradeoff between vascular and non-vascular cover. For the bog these results imply limitations on carbon uptake imposed by amounts of vascular cover between permafrost plateaus and collapse scar formations of different ages. At the fen the reverse is true and moss cover loss associated with the lowered water table is primary cause of a reduced ecosystem carbon sink.

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VIII. Literature cited

Aerts, R., & Ludwig, F. (1997). Water-table changes and nutritional status affect trace gas emissions from laboratory columns of peatland soils. *Soil Biology and Biochemistry, 29(11-12)*, 1691-1698.

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykanen, H., Martikainen, P.J. (1997). Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia, 110(3),* 423-431.

Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P. J., & Silvola, J. (1999). Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology, 80(1),* 161-174.

Blodau, C. (2002). Carbon cycling in peatlands — A review of processes and controls. *Environmental Review, 10(2)*, 111-134.

Bridgham, S. D., Patrick Megonigal, J., Keller, J. K., Bliss, N. B., & Trettin, C. (2006). The carbon balance of North American wetlands. *Wetlands, 26(4),* 889-916.

Bubier, J. (2003). Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochemical Cycles, 17(2)*, 1056

Bubier, J. L., Crill, P. M., Moore, T. R., Savage, K., & Varner, R. K. (1998). Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. *Global Biogeochemical Cycles, 12(4)*, 703-714.

Bubier, J. L., Frolking, S., Crill, P. M., & Linder, E. (1999). Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *Journal of Geophysical Research, 104(D22),* 27683-27692.

Camill, P. (1999). Patterns of boreal permafrost peatland vegetation across environmental gradients sensitive to climate warming. *Canadian Journal of Botany, 77(5)*, 721-733.

Camill, P., Lynch, J. A, Clark, J. S., Adams, J. B., & Jordan, B. (2001). Changes in biomass, aboveground net primary production, and peat accumulation following permafrost thaw in the boreal peatlands of Manitoba, Canada. *Ecosystems, 4(5)*, 461-478.

Chapin, F. S., McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., Kasischke, E. S., Euskirchen, E. S., Jones, J. B., Jorgenson, M. T., Kielland, K., Kofinas, G. P., Turetsky, M. R., Yarie, J., Lloyd, A. H., & Taylor, D. L. (2010). Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research, 40(7),* 1360-1370.

Chapin, F. S., Woodwell, G. M., Randerson, J. T., Rastetter, E. B., Lovett, G. M., Baldocchi, D. D., Clark, D. A., Harmon, M. E., Schimel, D. S., Valentini, R., Wirth, C., Aber, J. D., Cole, J. J., Goulden, M. L., Harden, J. W., Heimann, M., Howarth, R. W., Matson, P. A., McGuire, A. D., Melillo, J. M., Mooney, H. A., Neff, J. C., Houghton, R. A., Pace, M. L., Ryan, M. G., Running, S. W., Sala, O. E., Schlesinger, W. H., & Schulze, E. D. (2006). Reconciling carbon-cycle concepts, terminology, and methods. *Ecosystems, 9(7),* 1041-1050.

Chimner, R. A., & Cooper, D. J. (2003a). Carbon dynamics of pristine and hydrologically modified fens in the southern Rocky Mountains. *Canadian Journal of Botany, 81(5),* 477-491.

Chimner, R.A., & Cooper, D. J. (2003b). Influence of water table levels on CO_2 emissions in a Colorado subalpine fen: an in situ microcosm study. *Soil Biology and Biochemistry, 35(3),* 345-351.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2009). Effects of Experimental Water Table and Temperature Manipulations on Ecosystem CO_2 Fluxes in an Alaskan Rich Fen. *Ecosystems, 12(8),* 1329-1342.

Frolking, S., Roulet, N., & Fuglestvedt, J. (2006). How northern peatlands influence the Earth's radiative budget: Sustained methane emission versus sustained carbon sequestration. *Journal of Geophysical Research, 111(G1),* 1-10.

Frolking, S., & Roulet, N. T. (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology, 13(5),* 1079-1088.

Grosse, G., Harden, J., Turetsky M. R., McGuire, A. D., Camill, P., Tarnocai, C., Frolking, S., Schuur, E. A. G., Jorgenson, T., Marchenko, S., Romanovsky, V., Wickland, K., French, N., Waldrop, M., Bourgeau-Chavez, L., Striegl, R. G. (2011). Vulnerability of high latitude soil organic carbon in North America to

disturbance. *Journal of Geophysical Research Biogeosciences*, 116, G00K06, 23 pages.

Hinzman, L. D., Viereck, L. A., Adams, P. C., Romanovsky, V. E., & Yoshikawa, K. (2006). Climatic and permafrost dynamics of the Alaskan boreal forest. *Alaska's changing boreal forest* (pp. 0-34).

Holden, J. (2005). Peatland hydrology and carbon release: why small-scale process matters. *Philosophical Transactions of the Royal Society A*, *363(1837),* 2891-2913.

Hultén, E . (1968). Flora of Alaska and neighboring territories. Stanford Press, Stanford, CA.

Jorgenson, T. M., Racine, C. H., Walters, J. C., & Osterkamp, T. E. (2001). Permafrost degradation and ecological changes associated with a warming climate in central Alaska. *Climatic Change*, *48(4)*, 551-579.

Kane, E. S., Turetsky, M. R., Harden, J. W., McGuire, A. D., & Waddington, J. M. (2010). Seasonal ice and hydrologic controls on dissolved organic carbon and nitrogen concentrations in a boreal-rich fen. *Journal of Geophysical Research*, *115*, 1-15.

Lafleur, P. M., McCaughey, J. H., Joiner, D. W., Bartlett, P. A., & Jelinski, D. E. (1997). Seasonal trends in energy, water, and carbon dioxide fluxes at a northern boreal wetland. *Journal of Geophysical Research*, *102(D24),* 29009-29020.

Lafleur, P. M., Roulet, N. T., Bubier, J. L., Frolking, S. E., & Moore, T. R. (2003). Interannual variability in the peatland-atmosphere carbon dioxide exchange at an ombrotrophic bog. *Global Biogeochemical Cycles*, *17(2),* 1-14.

Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in Southern Finland. *The Journal of Applied Ecology*, *32(4),* 785.

Laine, J., Silvola, J., Tolonen, K., Alm, J., Nykänen, H., Sallantaus, T., Savolainen, I., et al. (1996). Effect of water-level drawdown on global climatic warmings: northern peatlands. *Ambio*, *25(3)*, 179-184.

Lawrence, C. (2010). Peat deformation in Alaskan peatlands: implications for peatland

vulnerability to drought. Unpublished Thesis. McMaster University. School of Geography and Earth Sciences.

Luken, J. O., & Billings, W. D. (1985). The influence of microtopographic heterogeneity on carbon dioxide efflux from a subarctic bog. *Ecography, 8(4),* 306-312.

McJannet, D. L., Vertessy, R. A., Tapper, N.J., O'Sullivan, S.K., Beringer, J., & Cleugh, H. (1996). Soil and litter evaporation beneath re-growth and old-growth mountain ash forest. Cooperative Research Centre for Catchment Hydrology, Clayton, Vic. Report 96/1

McLeod, M. (2004). Evaluation of an enclosed portable chamber to measure crop and pasture actual evapotranspiration at small scale. *Agricultural Water Management, 67(1),* 15-34.

Moore, T. R., Roulet, N. T., & Waddington, J. (1998). Uncertainity in predicting the effect of climatic change on the carbon cycling of Canadian peatlands. *Climatic Change, 40(2),* 229-245.

Muhr, J., Hohle, J., Otieno, D. O., & Borken, W. (2011). Manipulative lowering of the water table during summer does not affect CO_2 emissions and uptake in a fen in Germany. *Ecological Applications, 21(2),* 391-401.

Murphy, M., Laiho, R., & Moore, T. R. (2009). Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems, 12(8),* 1268-1282.

Myers-Smith, I. H., McGuire, A. D., Harden, J. W., & Chapin, F. S. (2007). Influence of disturbance on carbon exchange in a permafrost collapse and adjacent burned forest. *Journal of Geophysical Research, 112(G4),* 1-11.

Osterkamp, T. E., & Romanovsky, V. E. (1999). Evidence for warming and thawing of discontinuous permafrost in Alaska. *Permafrost and Periglacial Processes, 10(1),* 17-37.

Osterkamp, T. E., Viereck, L., Shur, Y., Jorgenson, M. T., Racine, C. H., Doyle, A. & Boone, R. D. (2000). Observations of Thermokarst and Its Impact on Boreal Forests in Alaska. *Arctic, Antarctic, and Alpine Research, 32(3),* 303-315.

Riordan, B., Verbyla, D., & McGuire, A. D. (2006). Shrinking ponds in subarctic Alaska based on 1950–2002 remotely sensed images. *Journal of Geophysical Research, 111(G4).*

Riutta, T., Laine, J., & Tuittila, E.-S. (2007). Sensitivity of CO_2 Exchange of Fen Ecosystem Components to Water Level Variation. *Ecosystems, 10(5),* 718-733.

Seppelt, R.D., Laursen, G.A., Lichvar, R.W. (2008). A guide to Alaskan black spruce wetland bryophytes: species specific to delineation for interior and south central regions. US Army Corps of Engineers.

Serreze, M. C., Walsh, J. E., Osterkamp, T., Dyurgerov, M., Romanovsky, V., Oechel, W. C., Morison, J., Zhang, T., & Barry, R.G. (2000). Observational evidence of recent change in the northern high-latitude environment. *Climatic Change, 46(1-2),* 159-207.

Shaver, G. R., Street, L. E., Rastetter, E. B., Van Wijk, M. T., & Williams, M. (2007). Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology, 95(4),* 802-817.

Tande, G. & Lipkin, R. (2003). Wetland sedges of Alaska. Alaska Natural Heritage Program Environment and Natural Resources Institute. Anchorage, AK.

Thormann, M. N., Bayley, S. E., & Szumigalski, A. R. (1998). Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta : Implications for global warming. *Hydrobiologia, 362(1-3),* 171-183.

Tuittila, E.S., Vasander, H., & Laine, J. (2004). Sensitivity of C sequestration in reintroduced Sphagnum to water-level variation in a cutaway peatland. *Restoration Ecology, 12(4),* 483-493.

Turetsky, M. R., Wieder, R. K., & Vitt, D. H. (2002). Boreal peatland C fluxes under varying permafrost regimes. *Soil Biology and Biochemistry, 34(7),* 907-912.

Turetsky, M. R., Wieder, R. K., Vitt, D. H., Evans, R. J., & Scott, K. D. (2007). The disappearance of relict permafrost in boreal North America: Effects on peatland carbon storage and fluxes. *Global Change Biology, 13(9),* 1922-1934.

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., & Harth, C. (2001). Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecological Applications, 11(2),* 311-326.

Vitt, D. H. (2006). Functional Characteristics and Indicators of Boreal Peatlands. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal Peatland Ecosystems* (Vol. 188, pp. 9-24). Springer-Verlag Berlin Heidelberg.

Vitt, D. H., & Chee, W.-L. (1990). The relationships of vegetation to surface water chemistry and peat chemistry in fens of Alberta, Canada. *Vegetatio, 89(2),* 87-106.

Vitt, D. H., Halsey, L. A, Bauer, I. E., & Campbell, C. (2000). Spatial and temporal trends in carbon storage of peatlands of continental western Canada through the Holocene. *Canadian Journal of Earth Sciences, 37(5),* 683-693.

Waddington, J. M., & Roulet, N. T. (1996). Atmosphere-wetland carbon exchanges: scale dependency of CO_2 and CH_4 exchange on the developmental topography of a peatland. *Global Biogeochemical Cycles, 10(2),* 233-245.

Wickland, K. P., Striegl, R. G., Neff, J. C., & Sachs, T. (2006). Effects of permafrost melting on CO_2 and CH_4 exchange of a poorly drained black spruce lowland. *Journal of Geophysical Research, 111(G2),* 1-13.

Wieder, R. K., Vitt, D. H., & Benscoter, B. W. (2006). Peatlands and the boreal forest. In R. K. Wieder & D. H. Vitt (Eds.), *Boreal Peatland Ecosystems* (Vol. 188, pp. 1-8). Springer-Verlag Berlin Heidelberg.

Wilson, D., Alm, J., Riutta, T., Laine, J., Byrne, K. A, Farrell, E. P., Tuitta, E.S. (2007). A high resolution green area index for modelling the seasonal dynamics of CO_2 exchange in peatland vascular plant communities. *Plant Ecology, 190(1),* 37-51.

Yoshikawa, K., & Hinzman, L. D. (2003). Shrinking thermokarst ponds and groundwater dynamics in discontinuous permafrost near council, Alaska. *Permafrost and Periglacial Processes, 14(2),* 151-160.

Yu, Z., Campbell, I. D., Campbell, C., Vitt, D. H., Bond, G. C., & Apps, M. J. (2003). Carbon sequestration in western Canadian peat highly sensitive to Holocene wet-dry climate cycles at millennial timescales. *The Holocene, 13(6),* 801-808.

IX. Figures and Tables

Table 3.1. Results from a repeated measures analysis of variance examining fluxes of gross primary productivity collected weekly from 2007-2010 for each water table manipulation plot at the fen, and from 2008-2010 at both collapse scar formations and intact permafrost at the bog.

Site		df (numerator, denominator)	F	P
Bog	Year	2,32	2.51	0.0975
	Plot	2, 25	8.97	0.0012
	Year x Plot	4, 32	18.77	< 0.0001
Fen	Year	3, 18	9.36	0.0006
	Plot	2, 6	24.62	0.0013
	Year x Plot	6, 18	3.38	0.0207

Table 3.2. Results from multiple comparison of the influence of year on fluxes of gross primary productivity collected weekly from 2007-2010 for each water table manipulation at the fen.

Years	Climate Conditions	df	t	*p*
2007 vs. 2009	Average climate vs. post flood	18	3.18	0.0242
2008 vs. 2008	Pre-flood vs. post-flood	18	3.15	0.0257
2008 vs. 2010	Pre-flood vs. drought	18	-3.07	0.0307
2009 vs. 2010	Post-flood vs. drought	18	-5.23	0.0003

Table 3.3. Estimated parameters from modeling Gross Primary Productivity following Equation 1 at the bog and fen plots. Estimates are provided for each plot using rates of GPP quantified under all light level conditions. All values in table are means ± SE, and all models were significant at $p < 0.0001$.

Site	Plot	$P_{max\ (PAR,WT)}$ ($\mu mol\ CO_2\ m^{-2}\ s^{-1}$)		k ($\mu mol\ m^{-2}\ s^{-1}$)		uP (cm)		tP (cm)		R^2
Bog	Permafrost	5.548	3.12	162.2	44.2	-79.7	77.9	57.2	46.5	0.78
	New collapse	6.312	0.41	286.9	56.3	5.7	0.9	17.3	1.6	0.80
	Old collapse	3.665	0.23	323.3	64.9	-1.3	2.2	24.0	6.9	0.86
Fen	Control	6.644	0.60	251.6	68.6	8.2	3.7	26.5	5.2	0.78
	Lowered	4.233	0.41	280.9	74.2	-17.9	13.7	88.1	20.4	0.81
	Raised	6.944	0.55	294.8	78.3	0.9	1.3	18.1	2.2	0.81

Table 3.4. Linear coefficients for regression ± SE between GPP and ET; all parameters were significant unless otherwise noted ($p < 0.0001$).

Site	Plot	Slope		Intercept		R^2
Bog	Permafrost	NS		0.105	0.012	0.02
	New collapse	-0.023	0.003	0.084	0.013	0.17
	Old collapse	-0.044	0.006	0.054	0.015	0.26
Fen	Control	-0.012	0.003	0.079	0.014	0.10
	Lowered	-0.026	0.005	0.046	0.015	0.29
	Raised	-0.019	0.003	0.058	0.016	0.26

Table 3.5. Estimated plant growth form group contributions to plot scale P_{max}, following Equation 2 where % cover (mosses) or VGA (vascular) is multiplied by the unique parameter associated with each plant growth form group: units are in terms of optimized photosynthesis per plant growth form group. Environmental parameters used in this model were as estimated from Equation 1, and reported in Table 2. Negative values are related to univariate relationships with GPP such that increases in a particular functional group decreases collar scale GPP. Proportion of explained variance is associated with both inclusion of vegetation parameters and previously estimated environmental parameters.

Site	Plot	V_{brown}* % Cover	$V_{dicranum}$* % Cover	V_{dshrub}* VGA	V_{eshrub}* VGA	$V_{feather}$* % Cover	V_{forb}* VGA	V_{grass}* VGA	V_{sedge}* VGA	$V_{sphagnum}$* % Cover	R^2
Bog	Permafrost		0.51	0.26	-0.45	1.15	0.53		-0.04	2.13	0.87
	New collapse		0.06	0.02	-0.03	0.01	0.08		0.83	4.58	0.88
	Old collapse		0	0.03	-0.13	0.01	0.43		0.36	3.64	0.88
Fen	Control	-0.96		7.34			0.90	-0.41	-0.36	0.81	0.91
	Lowered	-0.22		1.52			1.22	1.23	0.83	-0.23	0.82
	Raised	0.79		1.70			1.43	1.07	0.45	0.23	0.67

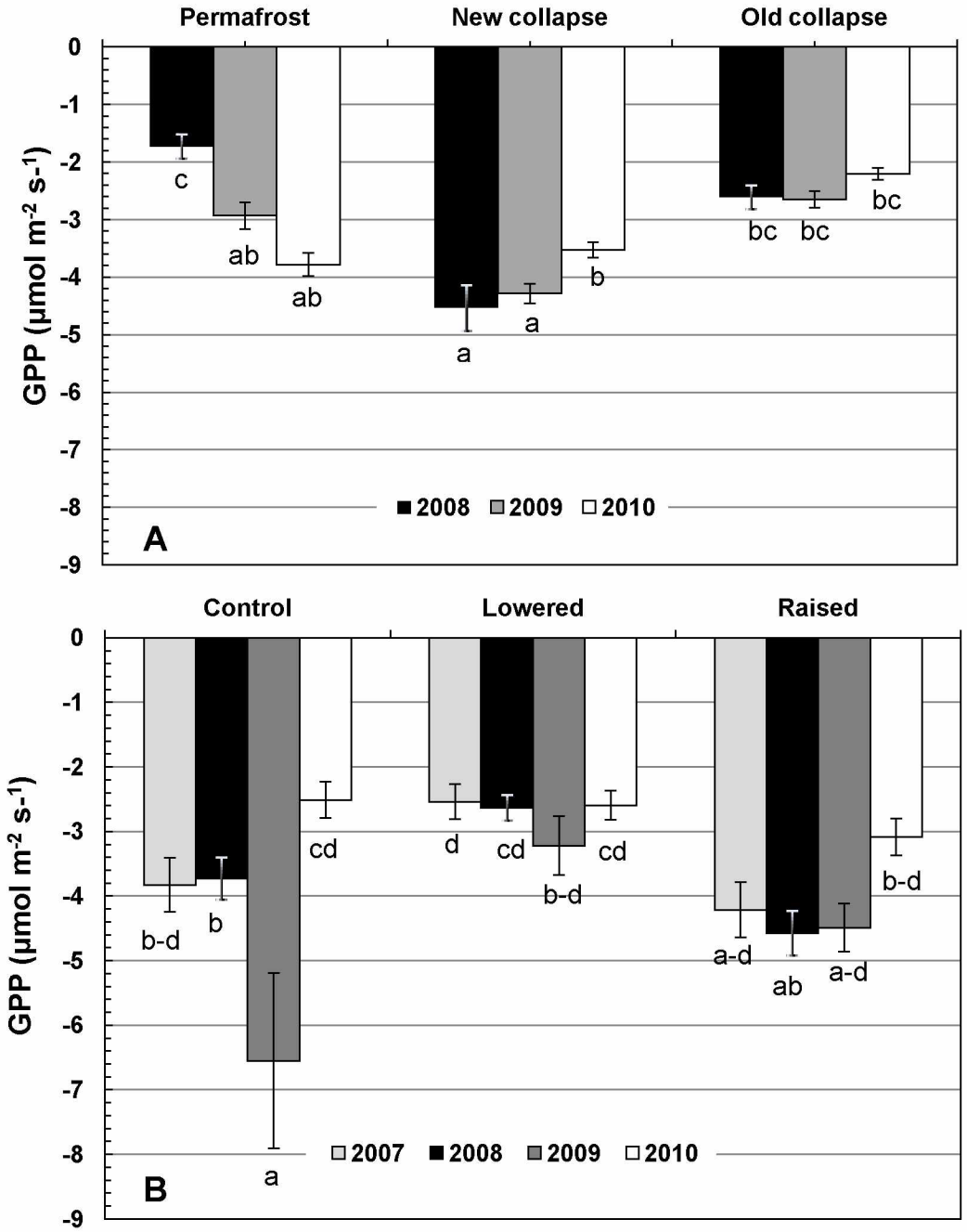

Figure 3.1. Mean annual comparisons of carbon uptake from the atmosphere, negative values represent greater uptake. Same letter designations indicate non-significant differences between plots and years. **A)** Annual GPP between collapse plots at the bog site and **B)** annual GPP at the water table manipulation plots of the fen site.

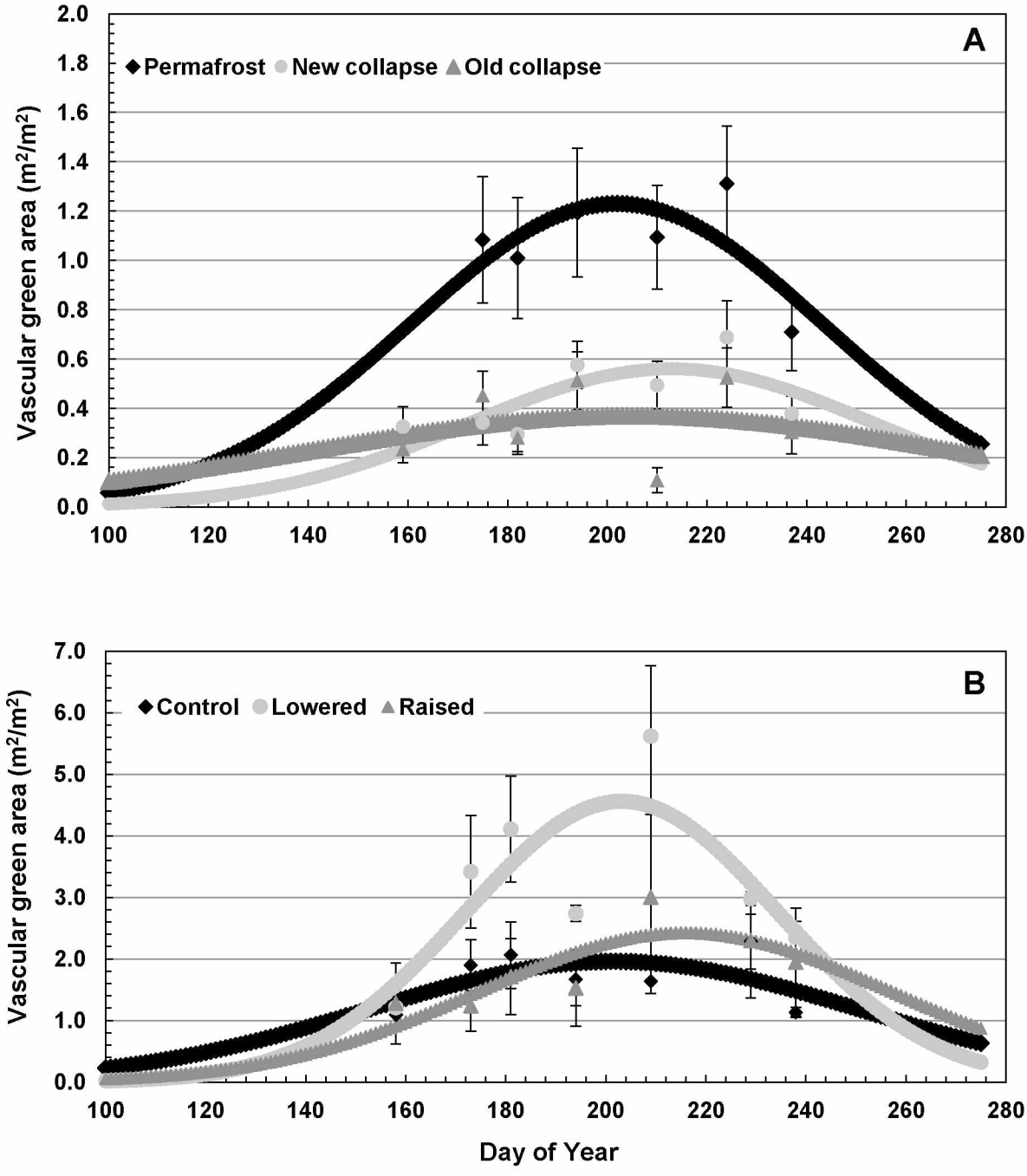

Figure 3.2. Measured daily VGA (m^2 / m^2; means ± SE) at the **A)** bog and **B)** fen sites for 2010. Modeled VGA following Wilson et al. (2007) are shown in the continuous curves.

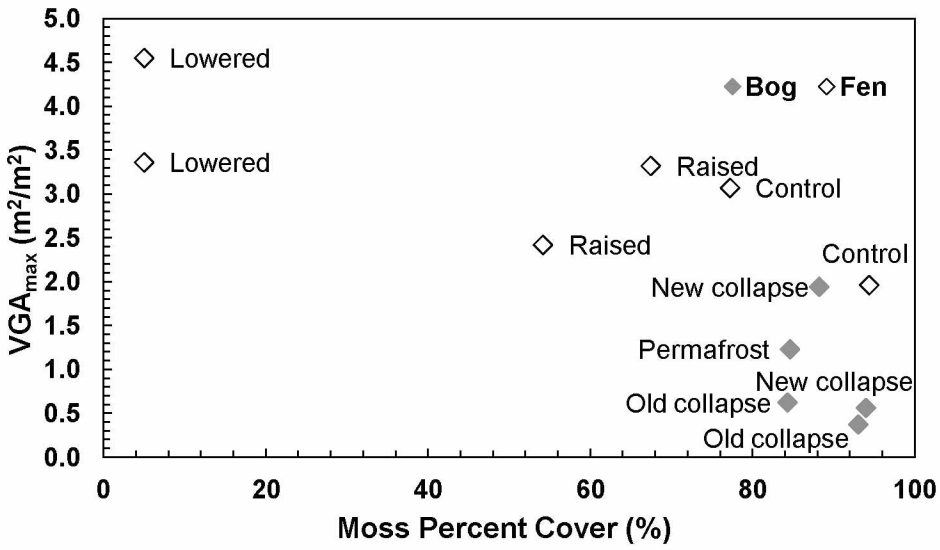

Figure 3.3. Relationship between VGA_{max} and percent ground cover of moss components of both peatland ecosystems for data collected 2009-2010.

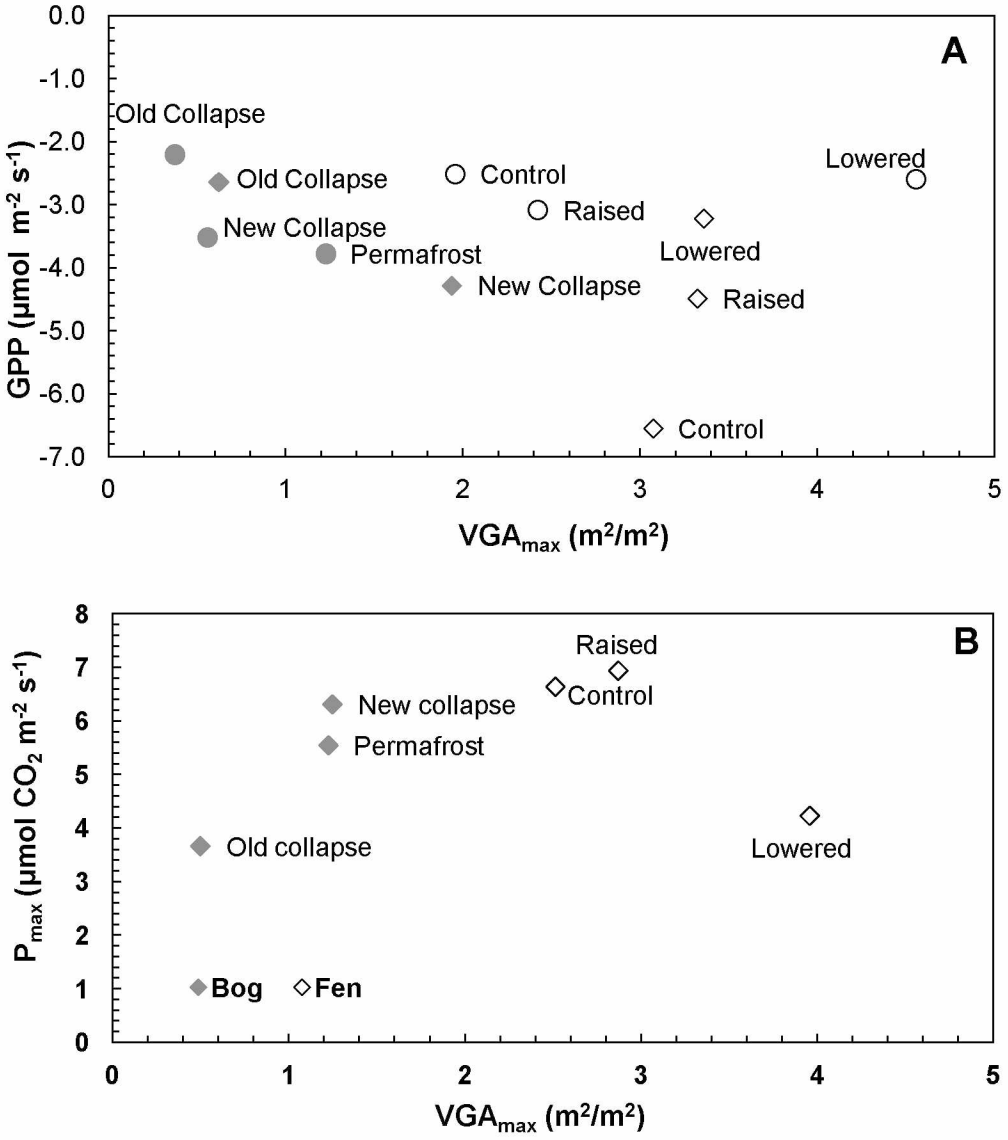

Figure 3.4. A) Relationship between ecosystem productivity function (GPP) and structure using VGA_{max} estimates from 2009 (diamonds) and 2010 (circles) with comparable plot annual averages at the bog (filled) and the fen (open). B) Relationship between P_{max} and VGA_{max} averaged across 2009 and 2010 at the bog and fen sites, with the exception of the permafrost plot where VGA_{max} data was only available from 2010.

X. Appendix

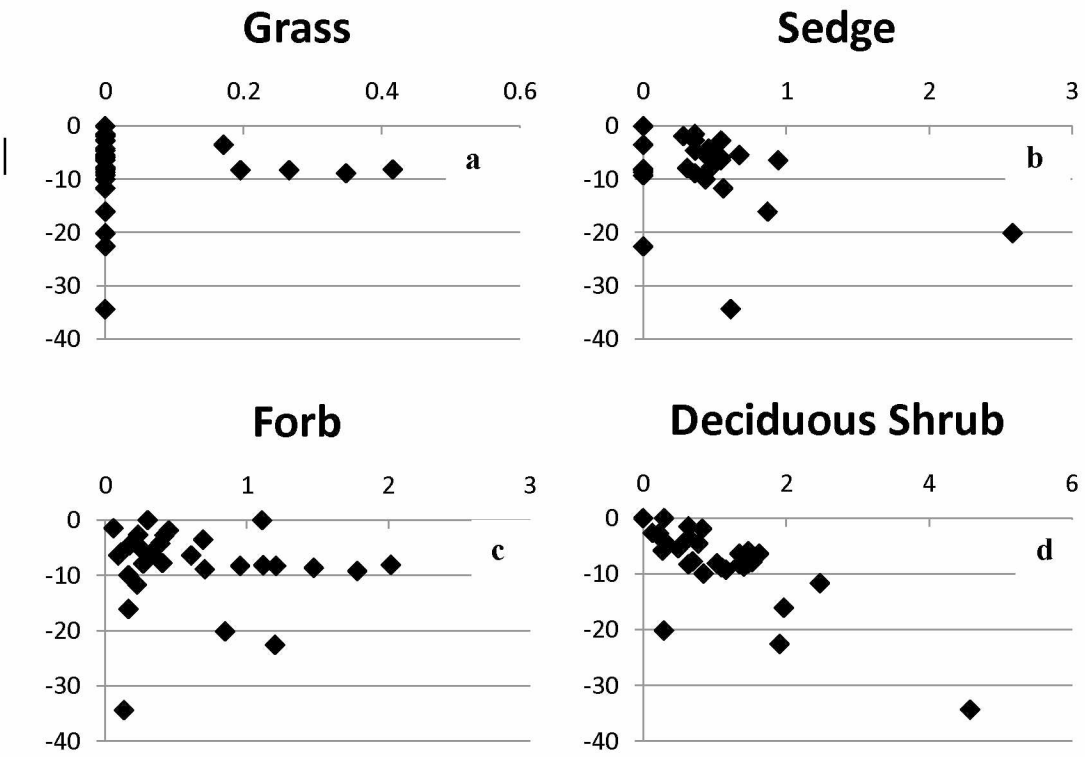

Figure A.1. Fen plant growth form (x axis- VGA m^2 / m^2) univariate relationships with GPP values standardized by environmental conditions (y axis- GPP µmol s^{-1} m^{-2}) for the control plot, including a) grasses, b) sedges, c) forbs and d) deciduous shrubs.

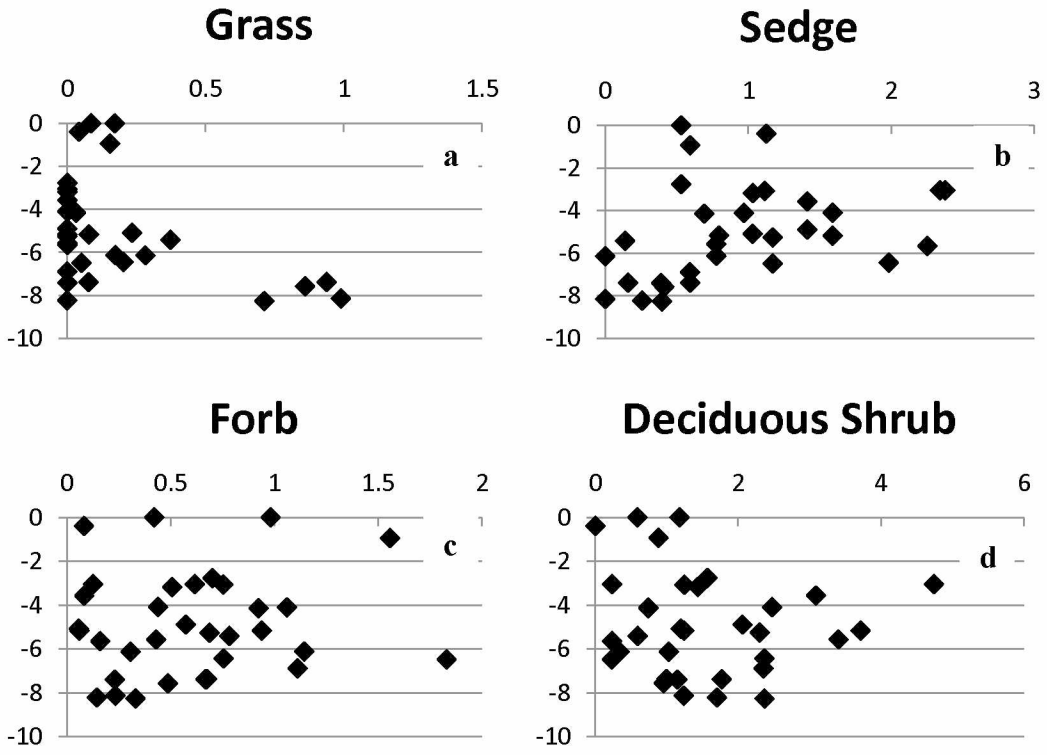

Figure A.2. Fen plant growth form (x axis- VGA m^2 / m^2) univariate relationships with GPP values standardized by environmental conditions (y axis- GPP µmol s^{-1} m^{-2}) for the lowered plot, including a) grasses, b) sedges, c) forbs and d) deciduous shrubs.

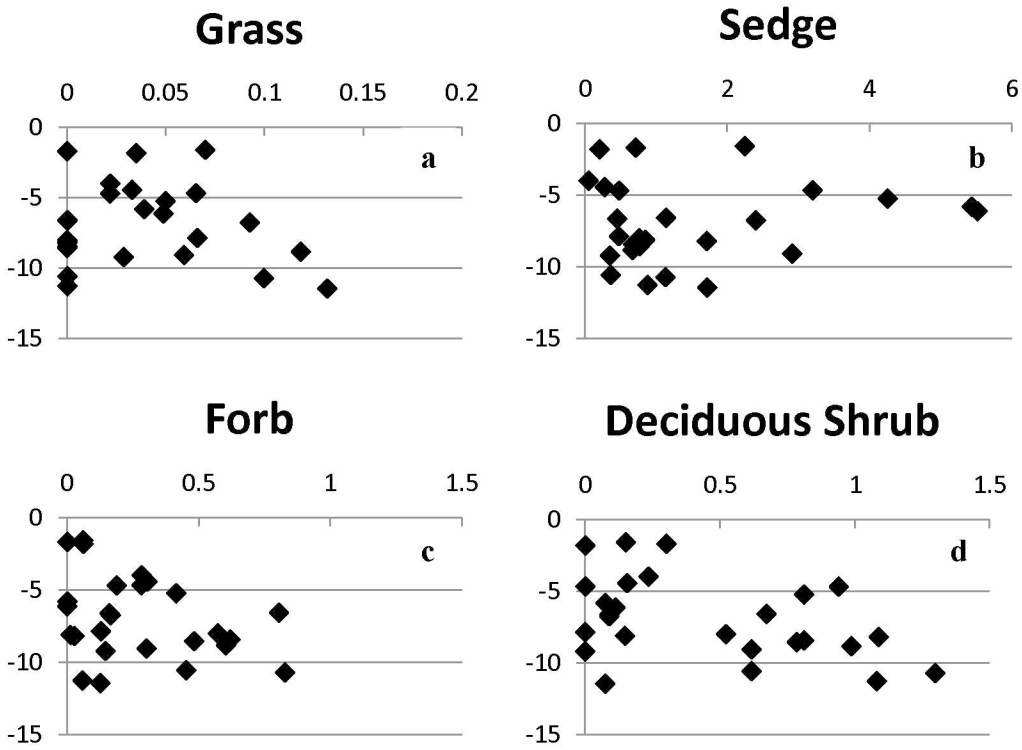

Figure A.3. Fen plant growth form (x axis- VGA m^2 / m^2) univariate relationships with GPP values standardized by environmental conditions (y axis- GPP μmol s^{-1} m^{-2}) for the raised plot, including a) grasses, b) sedges, c) forbs and d) deciduous shrubs.

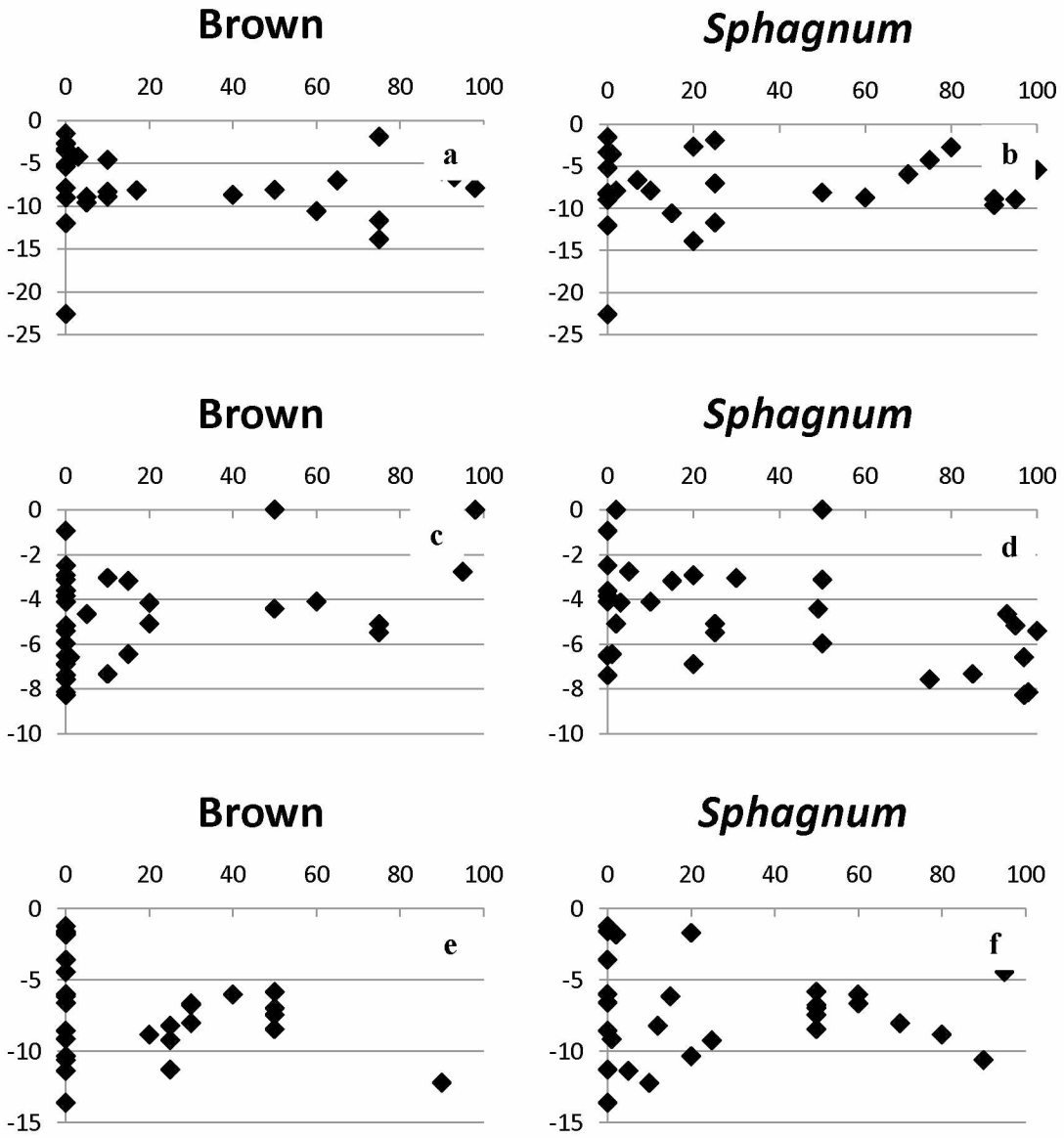

Figure A.3. Fen plant growth form (x axis- % Cover) univariate relationships with GPP values standardized by environmental conditions (y axis- GPP μmol s^{-1} m^{-2}) for the control plot moss growth forms a) brown moss and b) *Sphagnum*; the lowered plot moss growth forms c) brown moss and d) *Sphagnum*; and the raised plot moss growth forms e) brown moss and f) *Sphagnum*.

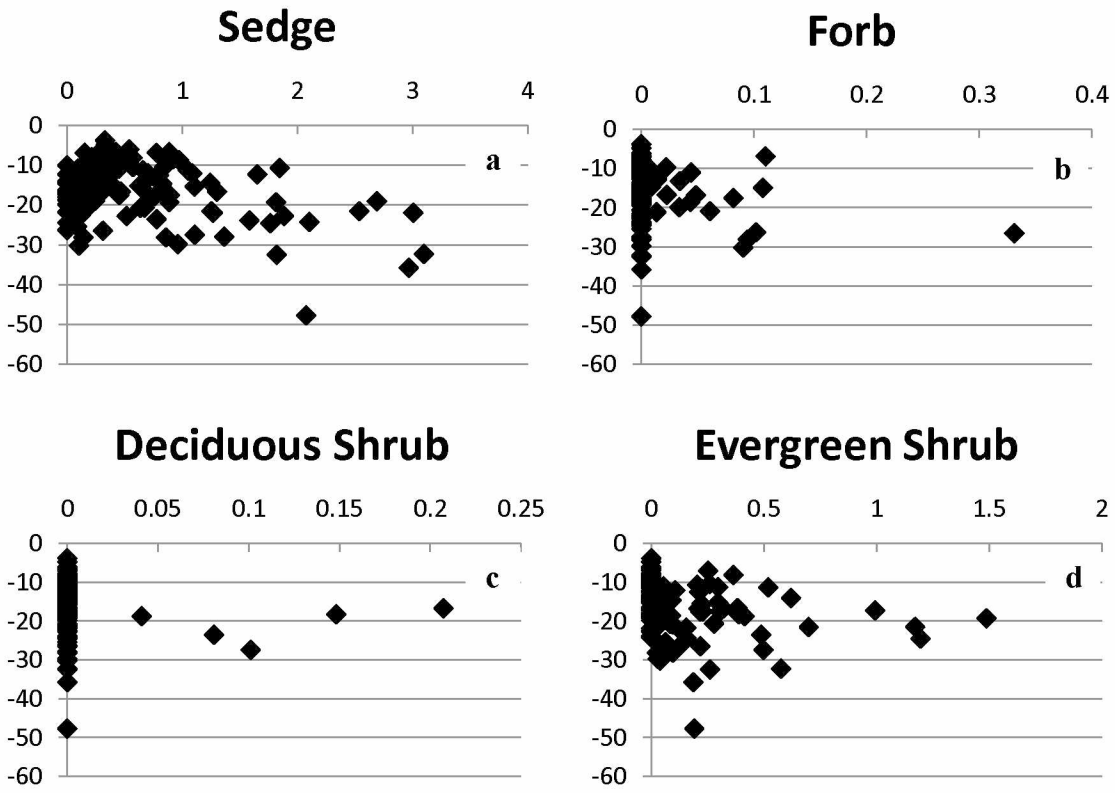

Figure A.4 Bog plant growth form univariate relationships with GPP values standardized by environmental conditions (x axis- VGA m^2 / m^2, y axis- GPP µmol s^{-1} m^{-2}) for the new collapse plot with a) sedges, b) forbs, c), deciduous shrubs and d) evergreen shrubs.

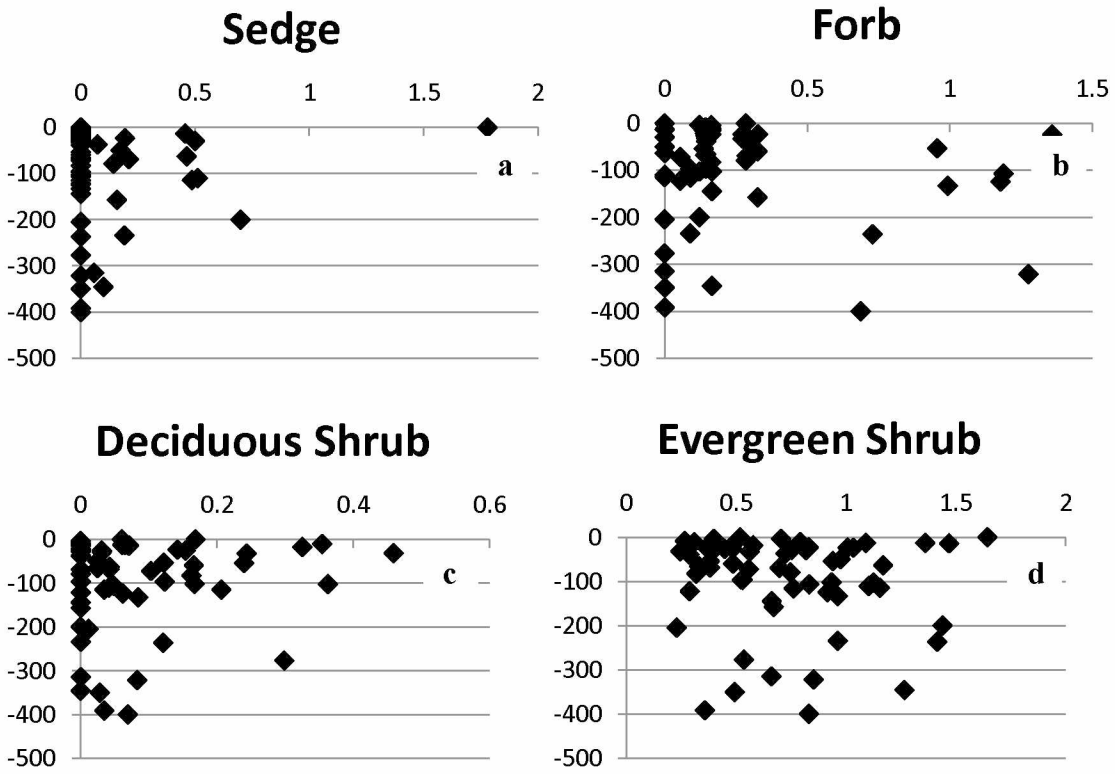

Figure A.5 Bog plant growth form univariate relationships with GPP values standardized by environmental conditions (x axis- VGA m^2 / m^2, y axis- GPP μmol s^{-1} m^{-2}) for the permafrost plot with a) sedges, b) forbs, c), deciduous shrubs and d) evergreen shrubs.

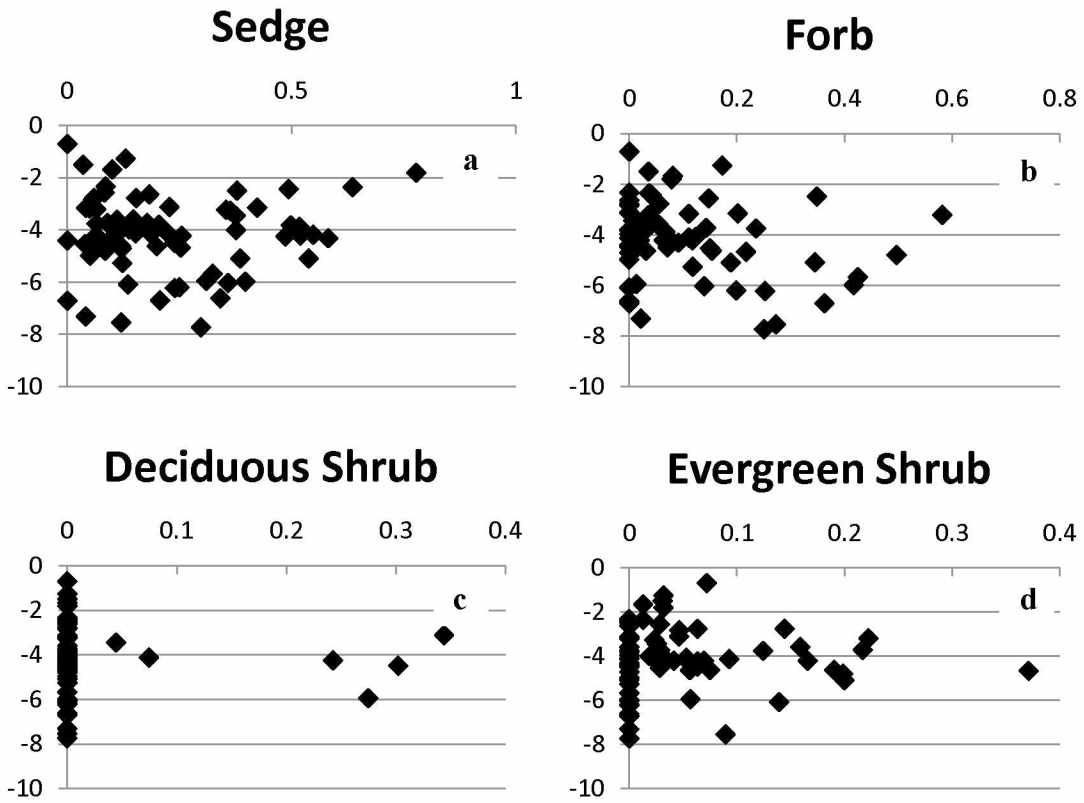

Figure A.6 Bog plant growth form univariate relationships with GPP values standardized by environmental conditions (x axis- VGA m^2 / m^2, y axis- GPP μmol s^{-1} m^{-2}) for the old collapse plot with a) sedges, b) forbs, c), deciduous shrubs and d) evergreen shrubs.

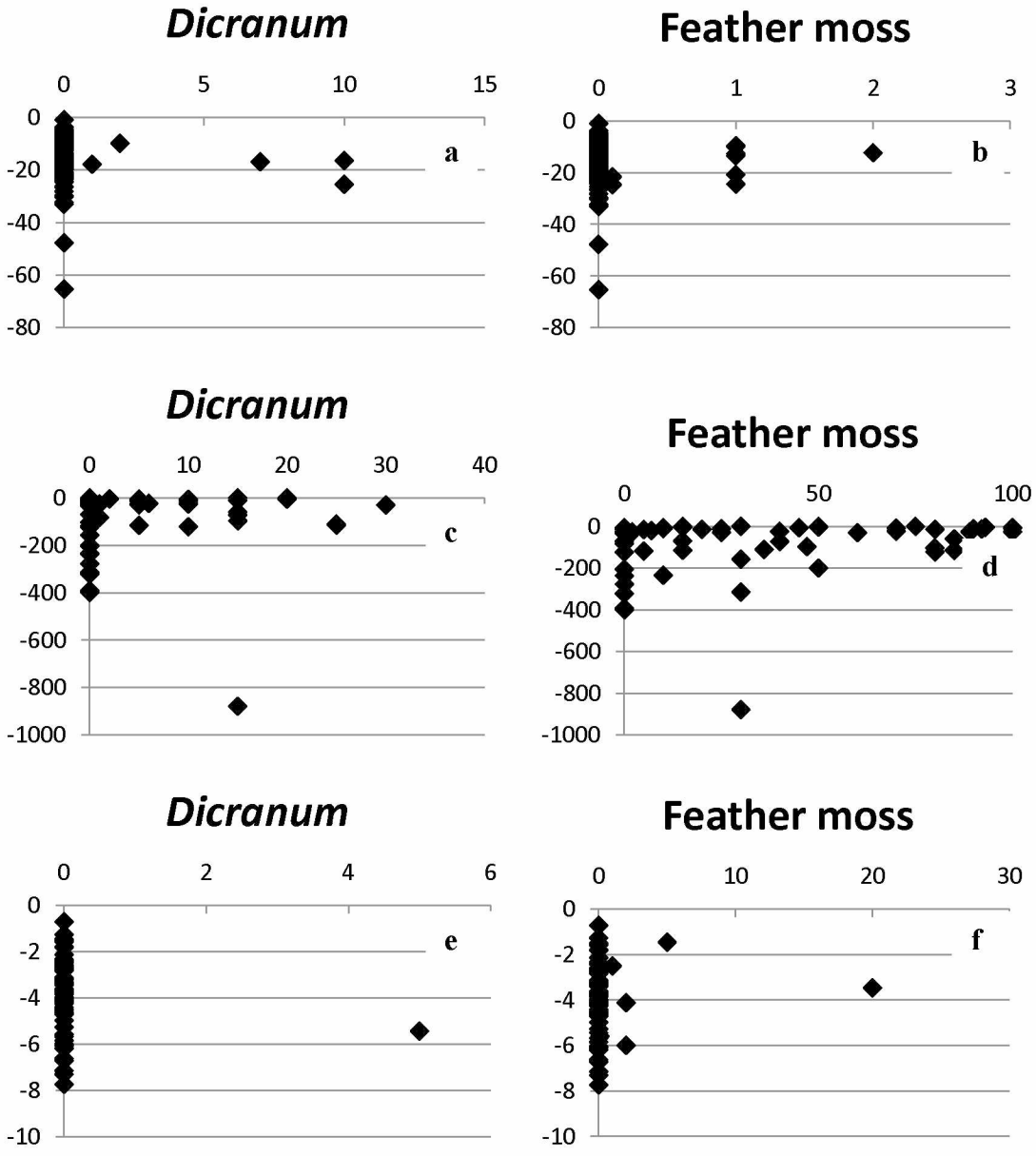

Figure A.7 Bog plant growth form univariate relationships with GPP values standardized by environmental conditions (x axis- % Cover, y axis- GPP μmol s^{-1} m^{-2}) moss type forms at the new collapse plot a) *Dicranum* and b) feather moss, at the permafrost plot c) *Dicranum* and d) feather moss and for the old collapse plot e) *Dicranum* and f) feather moss.

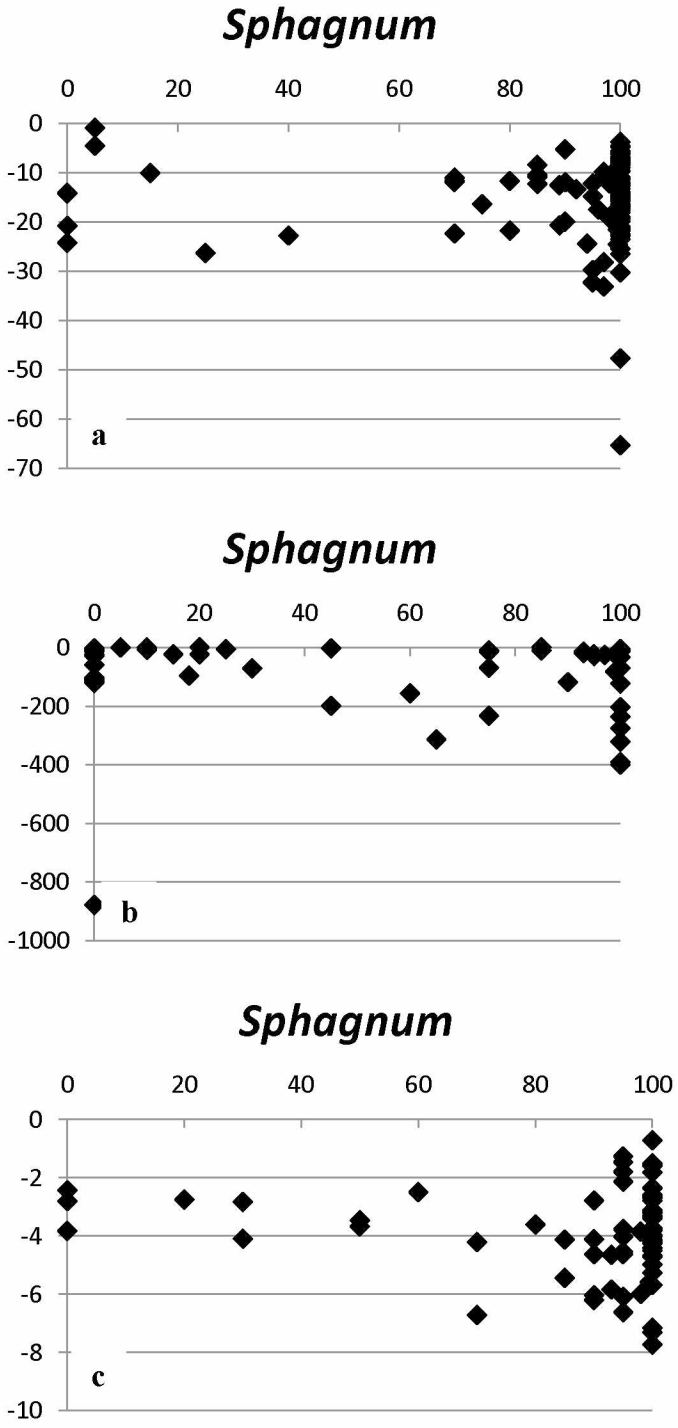

Figure A.8. Bog plant growth form univariate relationships with GPP values standardized by environmental conditions (x axis- % Cover, y axis- GPP μmol s^{-1} m^{-2}) for *Sphagnum* at a) the new collapse plot, b) the permafrost plot and c) the old collapse plot.

Chapter 4
I. Conclusions

Numerous studies in peatlands have reported annual shifts in carbon uptake or loss dependent on changing environmental conditions (Bubier et al., 1998; Bubier et al., 1999). Despite this significant annual variation, northern peatlands have historically accumulated carbon since initiation in the Holocene (Frolking and Roulet, 2007). Current and future predictions of rising air temperatures across the boreal region, however, have the potential to substantially alter processes that affect carbon dynamics (Chapin et al., 2010; Frolking and Roulet, 2007; Schuur et al., 2008). Peatland contributions to continued carbon uptake are highly influenced by hydrologic disturbance associated with movement of the oxidation-reduction boundary through change in water table position, and directional change in climatic conditions may reduce or reverse the peatland carbon sink (Alm et al., 1999; Bubier et al., 2003).

Conceptually, changes in environmental conditions contribute to both long- and short-term ecosystem responses that influence species composition, community structure, and gas exchange at the leaf surface (i.e. gross primary productivity, GPP; **Figure 1.1**). Peatland studies frequently focus on changes in water availability as the main driver of environmental change, as water table position controls the oxidation/reduction boundary between anaerobic and aerobic respiration. There have been a variety of methods used for observing peatland response to change in water availability, ranging from laboratory based soil core manipulations, mesocosm experiments in a common garden (Weltzin et al., 2000; Updegraff et al., 2001), and in situ manipulation experiments (Chivers et al., 2009, Murphy et al., 2009) to observational studies of natural variation in environmental conditions (Bubier et al 1999, Thormann et al., 1998). Some of the main differences in results among these approaches are related to differences in the temporal scale at which the change in water availability occurs.

Long term studies generally report changes in species composition within the ecosystem throughout the duration of altered water availability (Laine et al, 1995). Conceptually, changes in water availability cause changes in species composition as

some species are able to perform better under the altered conditions, which in turn cause changes in community structure and rates of net primary productivity (NPP; **Figure 1.1**). Draining peatlands generally results in the loss of hydrophilic species, especially mosses, and an increase in woody and drought tolerant species. These changes generally result in similar or increased net primary productivity (NPP) as woody vascular cover increases, and coincide with a localized loss in species diversity. Flooding, frequently associated with thermokarst, favors hydrophilic mosses with high rates of NPP, but removes the over-story tree cover. Chapter 2 of this thesis focused on two main objectives relating to extended change in water availability: 1) the influence of thermokarst in a peatland plateau and how this affects plant community composition, structure and productivity, and 2) differences between flooding and draining environmental conditions in causing changes in plant species composition and productivity in a fen.

Short term studies examining a response in GPP have generally found that decreasing water availability causes a reduction in GPP, while increasing water availability increases GPP (Chivers et al., 2009). As the change in water availability is maintained in these studies, the change in GPP will cause changes in net primary production (NPP) and vascular green area (VGA). Chapter 3 of this thesis focused on these interactions by examining: 1) the effect of hydrologic disturbance on GPP within and between a bog and fen, 2) the potential differences in the effects of environmental controls on GPP within a bog and fen in response to hydrologic disturbance, and 3) the influence of plant community structure on GPP in both bog and fen between types of hydrological disturbance.

The first objective in Chapter 2 addressed both how thermokarst in a peatland plateau bog may affect plant community composition, structure and productivity, and how these might change when considering time since thaw. My results indicated that thermokarst-associated flooding at the bog site altered the species composition between the permafrost plateau and collapse scars primarily associated with a loss in evergreen and deciduous trees, and an increase in sedges. Between the collapse formations, the old collapse (~ 45 years) contained more deciduous shrubs than the new collapse (~ 25

years). Structural changes in aboveground biomass were also evident within the peat plateau collapses, as total biomass decreased primarily associated with loss of trees, lichens, evergreen and deciduous shrubs. While total NPP was not different between the permafrost plateau and collapse formations there were differences in the relative contributions of plant growth forms. Moss productivity was greater in the collapse formations than in the permafrost plateau, but this increase was associated only with the new collapse. In general, moss productivity contributed 50% of total NPP in the old collapse, 58% in the permafrost plot and 76% in the new collapse. Vascular NPP was greater in the old collapse than the new collapse.

The second objective of chapter 2 focused on differences in response to flooding or drying of a moderate rich fen, and examining changes in plant species composition and productivity. I found that after 5 years of manipulation both flooding and drying hydrologic manipulations have significantly altered the vegetation composition in comparison to the control plot, through gains and losses in sedge richness and abundance. No structural differences in biomass or NPP were found; however there was a trend for increased vascular green area in the lowered water table manipulation at the expense of moss cover. Tradeoffs between growth forms and high variability associated with measurements in this study suggest that significant changes are likely as the manipulation continues. Additionally, comparisons involving structural measurements suggest that non-destructive methods of estimating abundance can be used to also estimate aboveground productivity and biomass, thereby allowing continuing monitoring of change in structure without degrading the peatland within each manipulation plot.

For Chapter 3 of my thesis I focused on ecosystem level responses to the same hydrologic conditions as examined in chapter 2. My first objective was to examine the variation in GPP between a moderate rich fen and a bog, and how these rates were influenced by hydrologic disturbance within each site. Comparison of GPP between plots without hydrologic disturbance, the permafrost plot at the bog and the control plot at the fen site, agreed with previous studies that found that fens assimilate more carbon than bogs (Bubier et al., 1998). Rates of carbon uptake were greater in the control plot of the

fen as compared with the permafrost plot at the bog, except for 2010 which was a dry summer with little groundwater recharge at the fen. Inter-annual differences in this study were primarily associated with seasonal changes in water table position. For example, the control plot at the fen showed an increase in GPP with a rise in water table, and a decrease with a decline in the water table. Responses of the permafrost plot at the bog were more complex, possibly associated with water storage in deeper peat that was accessed in the drier years following significant precipitation events.

Hydrologic disturbance associated with collapse scar formation at the bog site prompted significantly greater GPP uptake. However, GPP was significantly different between the new and old collapse scars. Although my measurements indicate that hydrologic disturbance at the bog resulted in the greatest GPP at the new collapse, it is likely that the permafrost plot has higher rates of carbon uptake because my GPP estimate of the permafrost plot does not include tree GPP. Fen water table manipulation plots remained consistent in hierarchy of carbon uptake with raised > control > lowered for the duration of the study. I found that hydrologic disturbance at the fen resulted in the reduced GPP at the lowered water table plot.

The second objective of chapter 3 was to examine the influence of environmental controls on GPP, and how these may vary between the bog and fen and across types of disturbance within each site. I applied a non-linear model including light levels and water table position to examine differences between plots within a site (Chivers et al., 2009, Tuittila et al., 2004). Estimates of light saturation (k) at the bog site followed a pattern of permafrost < new collapse < old collapse plots, while optimum water table position for GPP followed a pattern of permafrost < old collapse < new collapse plots. Environmental parameters associated with light saturated photosynthesis at optimum water table position (P_{max}) at the fen site did not vary significantly among water table manipulation plots, which was likely related to substantial natural variation that occured during the 4 year study.

My final objective in chapter 3 examined plant community controls on GPP, and how the contribution of different plant growth forms vary among plots of hydrologic

disturbance within the bog and fen. Previous work has shown that the relative contribution of vegetation communities associated with microforms in peatlands to GPP changes in response to hydrologic in northern peatlands (Alm et al., 1997; Alm et al., 1999; Bubier et al., 2003). However these previous comparisons were not designed to address functional changes in growth form or species composition as the plant community responds to disturbance. Partitioning of the carbon flux components has been studied in tundra systems (Shaver et al., 2007) and applied with some success in peatlands for relating cover and growth form contribution to ecosystem GPP (Ruitta et al., 2007; Tuitilla, et al., 2004). The parameter estimates from this study suggest that at the bog the moss layer is a main contributor to understory productivity, whether or not there is a presence of permafrost. Individual differences between plots were related to differences in abundance between forbs, sedges and deciduous shrubs. At the fen the main contributor to productivity were the deciduous shrubs, with plot differences in contributions from forbs, grasses and sedges.

Results from this study are potentially limited by site- dependent conclusions associated with measuring ecosystem primary production responses in one fen and one peat plateau bog. Extending these findings to similar systems would help elucidate implications of hydrological disturbance in peatlands for the climate system. For the bog site, functional and compositional differences were associated with the age of collapse scar formation, suggesting that more comprehensive studies of vegetation succession after permafrost collapse should be conducted. At the fen, while a change in species composition has occurred 5 years after the initiation of a water table manipulation, subtle changes have occurred in plant functional components, and continued monitoring is needed to further document change in the plant communities. Future work to understand the influence of hydrologic disturbance in peatlands should focus on improving the understanding of how responses in plant community composition affect carbon uptake.

II. Literature cited

Alm, J., Talanov, A., Saarnio, S., Silvola, J., Ikkonen, E., Aaltonen, H., Nykänen, H., & Martikainen, P. J. (1997). Reconstruction of the carbon balance for microsites in a boreal oligotrophic pine fen, Finland. *Oecologia*, *110(3)*, 423-431.

Alm, J., Schulman, L., Walden, J., Nykänen, H., Martikainen, P. J., & Silvola, J. (1999). Carbon balance of a boreal bog during a year with an exceptionally dry summer. *Ecology*, *80(1)*, 161-174.

Bubier, J. L., Crill, P. M., Moore, T. R., Savage, K., & Varner, R. K. (1998). Seasonal patterns and controls on net ecosystem CO_2 exchange in a boreal peatland complex. *Global Biogeochemical Cycles*, *12(4)*, 703-714.

Bubier, J. L., Frolking, S., Crill, P. M., & Linder, E. (1999). Net ecosystem productivity and its uncertainty in a diverse boreal peatland. *Journal of Geophysical Research*, *104(D22)*, 27683-27692.

Bubier, J. (2003). Peatland responses to varying interannual moisture conditions as measured by automatic CO_2 chambers. *Global Biogeochemical Cycles*, *17(2)*.

Chapin, F. S., McGuire, A. D., Ruess, R. W., Hollingsworth, T. N., Mack, M. C., Johnstone, J. F., Kasischke, E. S., et al. (2010). Resilience of Alaska's boreal forest to climatic change. *Canadian Journal of Forest Research*, *40(7)*, 1360-1370.

Chivers, M. R., Turetsky, M. R., Waddington, J. M., Harden, J. W., & McGuire, A. D. (2009). Effects of experimental water table and temperature manipulations on ecosystem CO_2 fluxes in an Alaskan rich fen. *Ecosystems*, *12(8)*, 1329-1342.

Frolking, S., & Roulet, N. T. (2007). Holocene radiative forcing impact of northern peatland carbon accumulation and methane emissions. *Global Change Biology*, *13(5)*, 1079-1088.

Laine, J., Vasander, H., & Laiho, R. (1995). Long-term effects of water level drawdown on the vegetation of drained pine mires in southern Finland. *The Journal of Applied Ecology*, *32(4)*, 785.

Murphy, M., Laiho, R., & Moore, T. R. (2009). Effects of water table drawdown on root production and aboveground biomass in a boreal bog. *Ecosystems*, *12(8)*, 1268-1282.

Riutta, T., Laine, J., & Tuittila, E.-S. (2007). Sensitivity of CO_2 exchange of fen ecosystem components to water level variation. *Ecosystems*, *10(5)*, 718-733.

Schuur, E. A. G., Bockheim, J., Canadell, J. G., Euskirchen, E., Field, C. B., Goryachkin, S. V., Hagemann, S., Kuhry, P., Lafleua, P. M., Lee, H., Mazhitova, G., Nelson, F. E., Rinke, A., Romanovsky, V. E., Shiklomanov, N., Tarnocai, C., Venevsky, S., Vogel, J.,& Zimov, S. A.. (2008). Vulnerability of Permafrost Carbon to Climate Change: Implications for the Global Carbon Cycle. *BioScience*, *58(8)*, 701-714.

Shaver, G. R., Street, L. E., Rastetter, E. B., Van Wijk, M. T., & Williams, M. (2007). Functional convergence in regulation of net CO_2 flux in heterogeneous tundra landscapes in Alaska and Sweden. *Journal of Ecology*, *95(4)*, 802-817.

Thormann, M. N., Bayley, S. E., & Szumigalski, A. R. (1998). Effects of hydrologic changes on aboveground production and surface water chemistry in two boreal peatlands in Alberta: Implications for global warming. *Hydrobiologia*, *362*, 171-183.

Tuittila, E. S., Vasander, H., & Laine, J. (2004). Sensitivity of C sequestration in reintroduced *Sphagnum* to water-level variation in a cutaway peatland. *Restoration Ecology*, *12(4)*, 483-493.

Updegraff, K., Bridgham, S. D., Pastor, J., Weishampel, P., & Harth, C. (2001). Response of CO_2 and CH_4 emissions from peatlands to warming and water table manipulation. *Ecological Applications*, *11(2)*, 311-326.

Weltzin, J. F., Pastor, J., Harth, C., Bridgham, S. D., Updegraff, K., & Chapin, C. T. (2000). Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, *81(12)*, 3464-3478.